LOWER CRETACEOUS (MIDDLE ALBIAN) AMMONITES FROM DOMBE GRANDE, ANGOLA

By

Michael R. Cooper

National Museum, Bulawayo

(With 31 figures)

[*MS accepted 3 March 1982*]

ABSTRACT

Two stratigraphically separated Middle Albian faunules, dominated by *Douvilleiceras* and *Oxytropidoceras* respectively, are described from the environs of Dombe Grande. The wide range of continuous variation within these assemblages has an important bearing on the taxonomy of these forms. The phylogeny of the Mojsisovicziinae is discussed, and the following new taxa are created: *Mortoniceratoides* gen. nov., *Oxytropidoceras (Mirapelia)* subgen. nov. and *O. (Benavidesites)* subgen. nov. Middle Albian biostratigraphy outside the Boreal Realm is discussed.

CONTENTS

INTRODUCTION

Choffat (*in* Choffat & De Loriol 1888) was the first to record ammonites from the lower part of the Albian succession of Angola, describing and figuring an '*Acanthoceras*' *mamillare* (Schlotheim) (= *Douvilleiceras mammillatum aequinodum* (Quenstedt)) (Choffat & De Loriol 1888: 71, pl. 3 (fig. 1)) from the Dombe Grande area. The specimen was said to have come from the 'Couches à *Pholadomya pleuromyaeformis*', but as these beds are almost certainly of Aptian age (Howarth 1965; Cooper 1976) this is an error. Howarth (1965) described a small collection of *Douvilleiceras* made in 1930–1 by Alexandre Borges from the Dombe Grande region, and recorded the species *D. mammillatum* var. *?aequinodum* (Quenstedt) and *D. orbignyi* Hyatt, thereby suggesting the presence of upper Lower Albian (*D. mammillatum* Zone) strata. Cooper (1976) described the bio- and lithostratigraphy of the region. The present collections come from the immediate vicinity of Dombe Grande

Ann. S. Afr. Mus. **89** (5), 1982: 265–314, 31 figs.

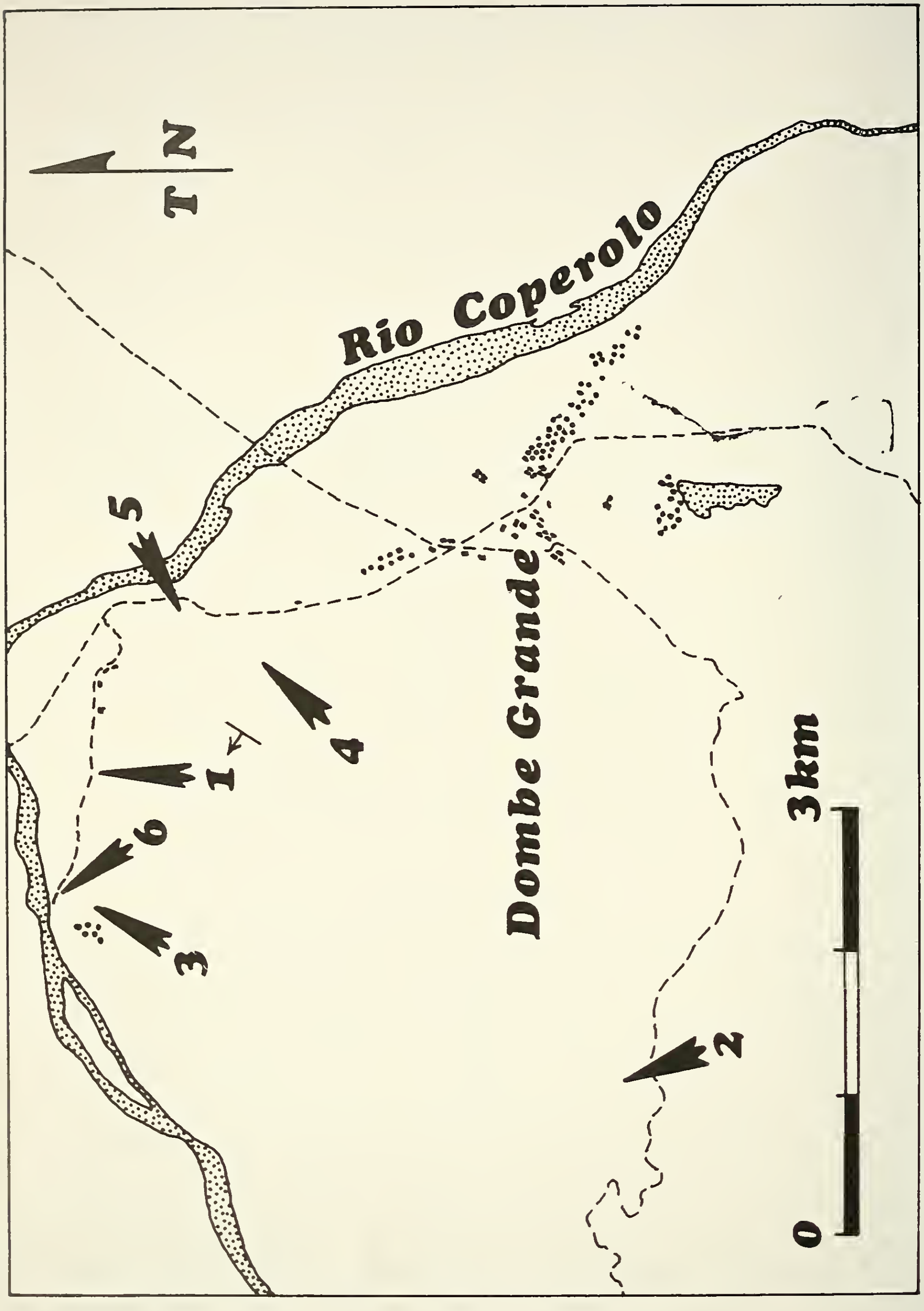

Fig. 1. Locality map, with collecting localities numbered. Broken lines represent roads.

(Fig. 1), and well above the beds containing *Pholadomya pleuromyaeformis* Choffat.

Prefixes to catalogue numbers refer to material in the following institutions:

BMNH	British Museum (Natural History), London
NHMP	Natural History Museum, Paris
OUM	Oxford University Museum, Oxford
SAM	South African Museum, Cape Town
USNMNH	U.S. National Museum of Natural History, Smithsonian Institution, Washington

Measurements are in millimetres, with dimensions, as a percentage of the diameter, in parentheses.

REGIONAL GEOLOGY

The late Mesozoic succession in the Cuanza basin has been named the Cuanza Group (Cooper 1976). At Dombe Grande in the extreme south of the basin (12°54′S 13°13′E), the base of the Cuanza sequence is formed by the Dombe Formation, a unit of coarse clastics and lagoonal deposits with interbedded evaporites. The disconformably overlying transgressive deposits of the 'Formação com *Pholadomya*' (Neto 1960, 1961) attain a thickness of about 100 m and comprise a basal member of oolitic limestones, calcarenites and siltstones capped by calcareous siltstones rich in *Pholadomya pleuromyaeformis* and other bivalves (Fig. 2C–F). Also present at this level are the echinoids *Salenia dombeensis* De Loriol and *Pygurus africanus* De Loriol, and the molluscs *Neithea shawi* Pervinquière, *Retusa malheiroi* (Choffat), *Panopea gurgitis* (Brongniart), *Lithophaga praelonga* (d'Orbigny), *Nerita malheiroi* Choffat, '*Natica*' *feioi* Choffat, *Actaeonella (Trochactaeon) cordeiroi* (Choffat), *Actaeon lenzi* Choffat, *Ampullina (Pseudamaura) bulbiformis* (J. Sowerby), *Pinna robinaldina* d'Orbigny, *Cylindrites? delgadoi* Choffat, and *Tylostoma peschueli* Choffat.

Marine regression is reflected in the succeeding 'Formação com *Nerinea*' (Fig. 1, locality 2), a lithologically highly variable unit spanning some 400 m and comprising red and yellow lagoonal clastics yielding fossil wood, the gastropods *Nerinea capelloi* Choffat (Fig. 3G–H) and *Cerithium monteiroi* Choffat, and an indeterminate ammonite (*fide* Neto 1961).

The 'Formação com *Nerinea*' are overlain, perhaps disconformably, by limestones and marls at the base of the Cuio Formation, the lower beds of which have yielded the faunas described herein. The two assemblages, which were picked up mainly as surface scree, are stratigraphically separated at locality 4 (Fig. 1), with the *Oxytropidoceras* fauna occurring to the north-east and thus from the younger beds. Upward the sequence becomes increasingly unfossiliferous, and calcarenites and grits (Fig. 1, locality 1) span much of the

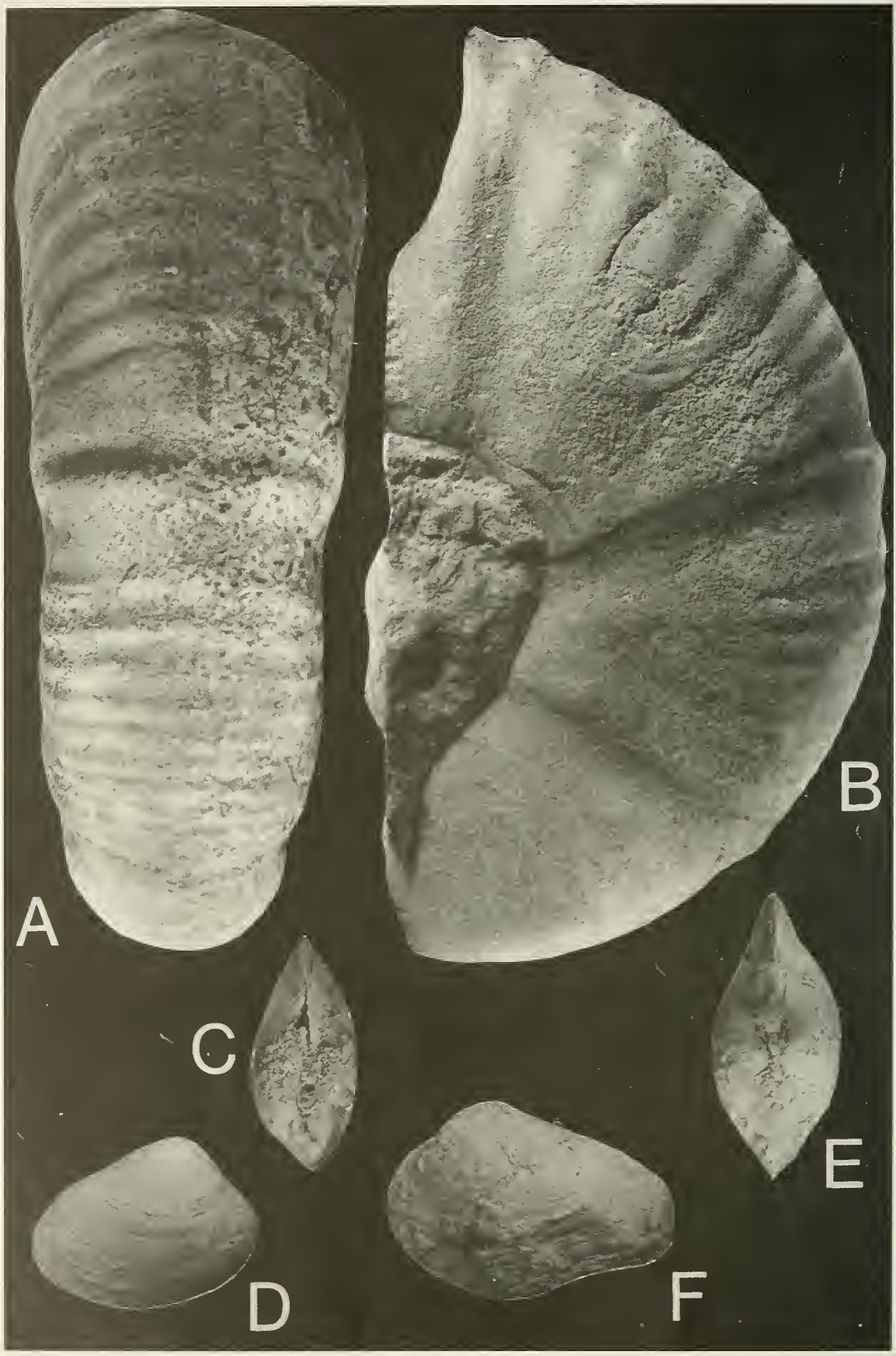

Fig. 2. A–B. *Puzosia bistricta* (White), SAM–PCA2649, × 1. C–F. Undetermined bivalves from the 'Couches a *Pholadomya*', Reinecke Collection, South African Museum, × 1.5.

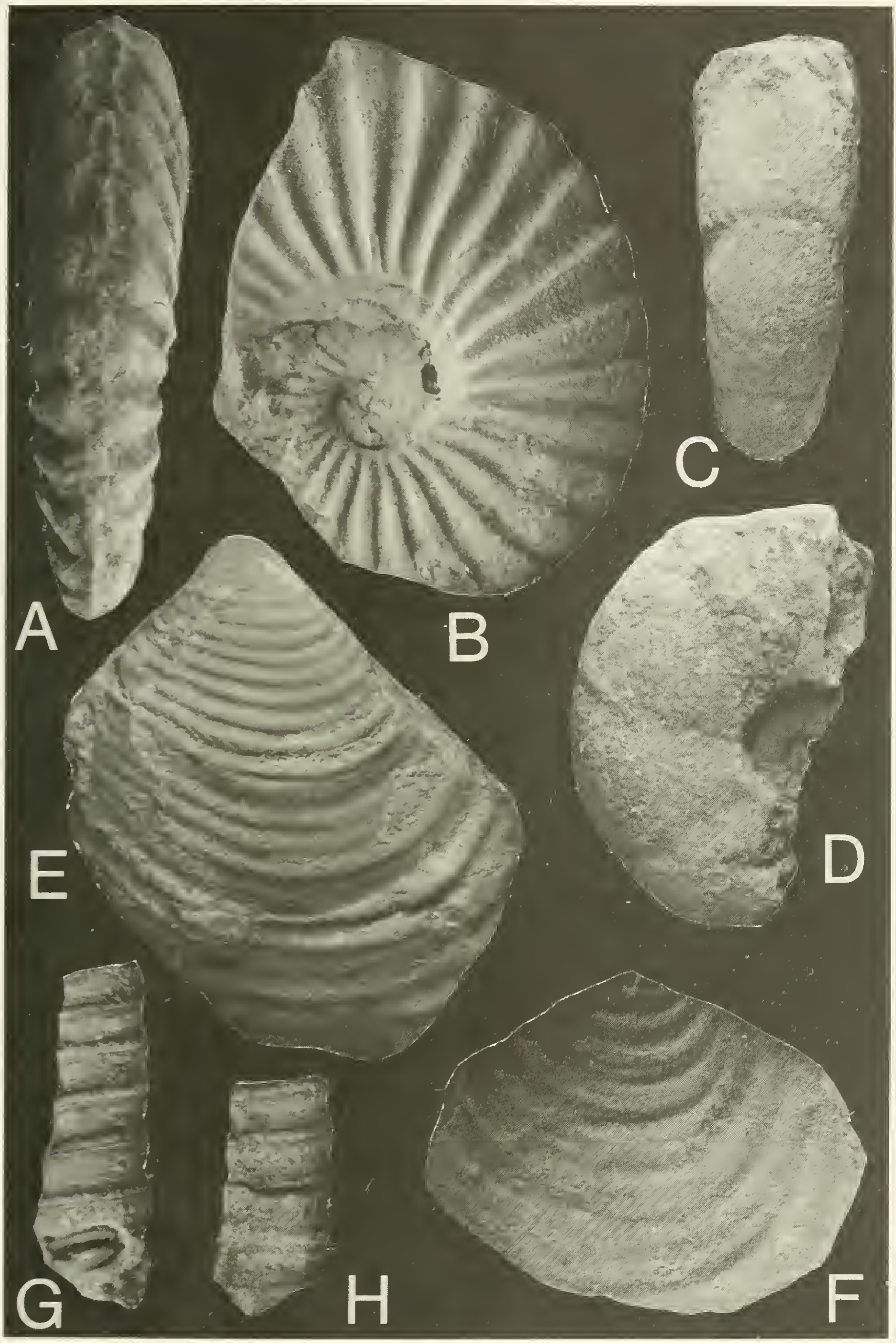

Fig. 3. A–B. *Oxytropidoceras (Mirapelia) buarquianum* (White), SAM–PCA5445, an individual transitional to *douglasi* morphotypes. C–D. *Puzosia bistricta* (White), SAM–PCA3474. E. *Inoceramus* gr. *anglicus* Woods, SAM–PCA3443, from the *Douvilleiceras* assemblage. F. *Birostrina?* cf. *coptensis* (Casey), SAM–PCA2664, from the *Oxytropidoceras* assemblage. G–H. *Nerinea capelloi* Choffat. G. SAM–PCA5448, × 1,5. H. SAM–PCA5450, × 1,5. All × 1 unless otherwise stated.

remainder of the Middle Albian. These sediments are interpreted as reflecting marine regression. The Cuio Formation attains a thickness of some 200 m and is succeeded by bioclastic and oolitic limestones and calcarenites (Fig. 1, localities 3, 6) yielding a low Upper Albian fauna including *Prohysteroceras wordiei* Spath and *Mortoniceras* spp. This unit is to be correlated with the Catumbela Member of the Cabo Ledo Formation to the north, reflecting the early late Albian (*Hysteroceras orbignyi* Zone) transgression.

SYSTEMATICS

Subclass AMMONOIDEA Zittel, 1884

Family **Douvilleiceratidae** Parona & Bonarelli, 1897

Discussion

Since the lineage *Procheloniceras* → *Cheloniceras* → *Eodouvilleiceras* → *Douvilleiceras* represents a single phyletic lineage, the subfamily Cheloniceratinae should be included in the synonymy of the nominate subfamily.

Subfamily **Douvilleiceratinae** Parona & Bonarelli, 1897

Genus *Douvilleiceras* de Grossouvre, 1894

Type species *Ammonites mammillatus* Schlotheim, 1813; subsequent designation of I.C.Z.N., Opinion 422, 1956

Discussion

Casey (1962: 260) has given a detailed diagnosis and discussion of this genus, to which little may be added.

The genus *Trinitoceras* was erected (Scott 1940: 1016) for very large douvilleiceratids in which the '. . . douvilleiceratid sculpture is evident up to or beyond a diameter of 200 mm. Costae are multituberculate as in *Douvilleiceras*, but the umbilical tubercles are greatly exaggerated in size, forming large bullae on the umbilical margin at the ends of alternate costae. On later whorls costae lose all trace of tuberculation but retain, irregularly, their alternate primary and secondary arrangement. On the latest whorls shown, the ribs are nearly equal, except that the occasional secondary (marked only by the fact that it does not reach the umbilicus) is intercalated between the primaries. The whorl section, degree of evolution, and the umbilical area do not differ greatly from like features of well-known species of *Douvilleiceras*.'

It is clear from the above description that the genus *Trinitoceras* is based upon the gigantic shells that accompany virtually all *Douvilleiceras* populations; thus *D. leightonense* Casey, *D. cheloniceratiforme* Tavani, *D. restitutum* Anderson, and *D. charshangense* Mirzoyev are all typical *Trinitoceras*. However, the fact that *Trinitoceras* and *Douvilleiceras* everywhere occur together as well as the fact that they are indistinguishable in their early ontogenetic stages and attain maturity at vastly different diameters, suggests to the writer that the differences are those between sexual dimorphs. *Trinitoceras* is here considered to be based upon *Douvilleiceras* macroconchs, and Casey (1962) is followed in regarding it a synonym of *Douvilleiceras*.

Up to now almost fifty trivial names have been applied to *Douvilleiceras*; these include *D. mammillatum* (Schlotheim) and its varieties *paucicostatum* Parona & Bonarelli, *praecox* Casey, *baylei* Spath and *aequinodum* (Quenstedt), *D. inaequinodum* (Quenstedt), *D. pseudinaequinodum* Collignon, *D. orbignyi* Hyatt, *D. clementinum* (d'Orbigny), *D. solitae* (d'Orbigny), *D. tarapacaense* Etayo-Serna, *D. abozaglio* Etayo-Serna, *D. ivernoisi* (Coquand), *D. spiniferum* (Whiteaves), *D. rex* (Scott), *D. reesidei* (Scott), *D. grandense* (Scott), *D. adkinsi* (Scott), *D? dunlapi* (Scott), *D. quitmanense* Scott, *D. spathi* Scott, *D. cuchillense* Scott, *D. muralense* Stoyanow, *D. aurarium* Anderson, *D. restitutum* Anderson, *D. offarcinatum* (White), *D. euzebioi* (Maury), *D. sergipense* Beurlen, *D. multinodosum* Hubach, *D. benonae* Besairie, *D. spinosum* Tavani, *D. albiense* (Tavani), *D. variabile* Tavani, *D. cheloniceratiforme* Tavani, *D. scabrosum* Casey, *D. alternans* Casey, *D. pustulosum* Casey, *D. leightonense* Casey and its variety *pringlei* Casey, *D. magnodosum* Casey, *D. subleightonense* Mirzoyev, and *D. charshangense* Mirzoyev.

The extreme range of morphological variation exhibited by most assemblages is emphasized by the splitting of the British collections into fourteen taxa (Casey 1962), those from Texas into eleven species (Scott 1940), and the Somali collections into eight species (Tavani 1942, 1949), and this seems to suggest genetic polymorphism. Thus Casey (1962: 263) has noted that all the mostly endemic species of *Douvilleiceras* recorded from southern England '. . . come from a limited range of strata and they constitute a closely interconnected plexus that in former days would have been interpreted (perhaps correctly) as one very large, highly variable species'. Unfortunately Casey's revision, coming at a time when it was the practice to base species on very narrowly defined limits, suffers from oversplitting, since recent studies of ammonite populations (Kennedy & Cobban 1976) suggests that such variation is not extraordinary. In addition, Mirzoyev (1967: 54) has also commented that '. . . all species of *Douvilleiceras* are closely interrelated and could have been treated as a single very extensive and varied species; but investigators concerned with this group of ammonites have made efforts to discover differences, based entirely on the frequency, degree of development and modifications of the conch sculpture in the course of its development'.

Casey (1962), in his revision of the British species of *Douvilleiceras*, laid much emphasis on the width of the ventral sulcus, number of notches per rib, and the ontogenetic stage at which ornament change occurred as taxonomic criteria. However, many writers have noted that the number of notches increases with diameter, while Collignon (1963), Mirzoyev (1967), and McLearn (1972) have all reported specimens with different numbers of notches on opposing flanks. Consequently, this criterion is considered to be of very limited taxonomic significance, if at all. Both the width of the ventral sulcus and the ontogenetic stage at which morphological changes occur are relative characters that are unlikely to stand up to population analysis, especially when it is considered that many of the taxa so defined are contemporaneous, occurring together in the same bed. As such, the writer believes *Douvilleiceras* to display genetic polymorphism and thus high intraspecific variability.

Stratigraphically *Douvilleiceras* ranges from the top of the *Leymeriella tardefurcata* Zone (*Leymeriella regularis* Subzone) into the lower part of the Middle Albian (*Lyelliceras lyelli* Subzone of the *Hoplites dentatus* Zone). During this period it attained a cosmopolitan distribution and is currently reported from North America (British Columbia, California, Arizona, Texas, New Mexico), South America (Peru, Columbia, Brazil), Africa (Gabon, Angola, Zululand, Mozambique, Somalia), Madagascar, Asia (eastern Carpathians, northern Caucasus, western and central Kopet Dag, Bol'shoy Balkhan, Tuarkyr, Mangyshlak, Badkhiz Islands, southern Gissar Range, Afghanistan), Europe (southern England, France, Switzerland, ?Germany, Poland, Bulgaria), and Japan.

Douvilleiceras mammillatum aequinodum (Quenstedt, 1849)

Figs 4A–B, 6C–G, 7D, G–I, 8A–B, 9A–C, E, 10C–D, F–H, 12A–B, 17A

Ammonites monile aequinodus Quenstedt, 1849: 137, pl. 10 (fig. 2).
? *Ammonites offarcinatus* White, 1887: 219, pl. 23 (fig. 4 only).
Acanthoceras mammillare (Schlotheim) Choffat (*in* Choffat & De Loriol), 1888: 71, pl. 3 (fig. 1).
Douvilleiceras monile var. *aequinodum* (Quenstedt) Breistroffer, 1947: 65.
? *Douvilleiceras cheloniceratiforme* Tavani, 1949: 38, pl. 8 (fig. 6).
? *Douvilleiceras monile* (J. Sowerby) Benavides-Cáceres, 1956: 442, pl. 43 (figs 1–4).
? *Douvilleiceras restitutum* Anderson, 1938: 175, pl. 54 (fig. 2).
Douvilleiceras mammillatum var. *aequinodum* (Quenstedt) Casey, 1962: 271, pl. 40 (fig. 5), pl. 41 (figs 5–7), pl. 42 (fig. 10), figs 94a–c, 95a–b, 102d, 103a–b. Howarth, 1965: 343, pl. 1 (figs 1–4).
? *Douvilleiceras albense* Spath, Collignon, 1963: 112, pl. 284 (fig. 1243).
Douvilleiceras sp. B, Beurlen, 1970: 460, pl. 4 (figs 3–4), figs 16–17.
? *Douvilleiceras spiniferum* (Whiteaves) McLearn, 1972: 62, pl. 28 (fig. 1 only).
Douvilleiceras cf. *mammillatum* (Schlotheim) Young, 1974: 184, pl. 4 (figs 1, 3, 6).

Material

Fifty-seven specimens, SAM–PCA2639, 3409, 3417, 3427, 3429–3431, 3434, 3439–3440, 3442, 3456, 3459–3460, 3462–3464, 3467, 3469, 3471–3473, 3476–3480, 3482, 3484–3487, 3490–3491, 3493–3494, 3499, 3501, 3503, 3509–3511, 3516–3518, 3520, 3522–3523, 3526–3527, 3529–3530, 3532, 3534, and 3536, all preserved as limestone steinkerns.

Description

This taxon is the most abundant component of the *Douvilleiceras* fauna, although many of the specimens are fragmentary and most are more or less eroded, having been picked up as surface scree. This erosion gives a number of

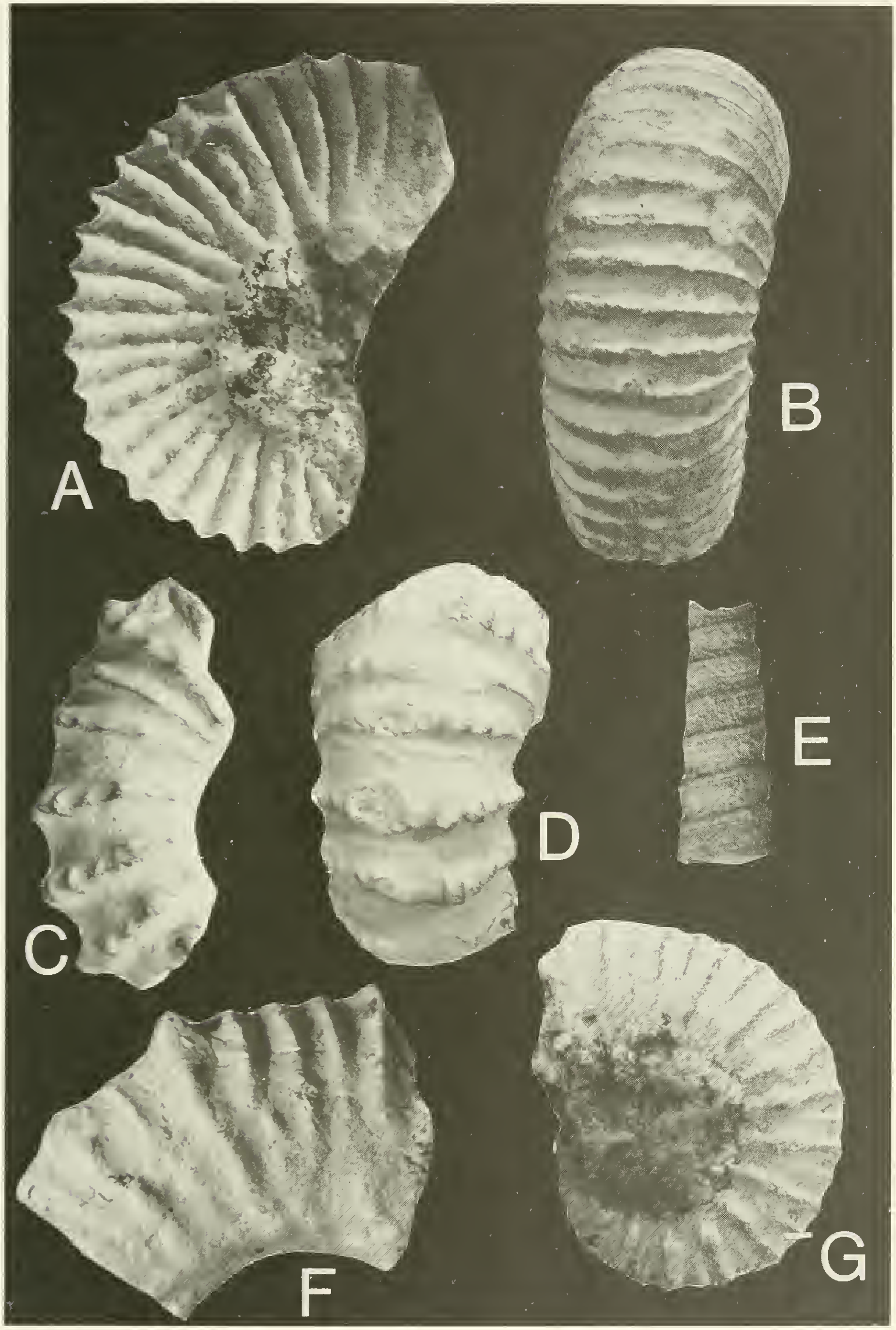

Fig. 4. A–B. *Douvilleiceras mammillatum aequinodum* (Quenstedt), SAM–PCA3434. C–D, F. *Douvilleiceras inaequinodum* (Quenstedt). C–D. SAM–PCA3435, a juvenile showing very fine intercalated ribs. F. SAM–PCA5451, a badly eroded fragment showing three intercalated ribs between main ribs. E. *Nerinea capelloi* Choffat, SAM–PCA5449, × 1,5. G. *Douvilleiceras variabile* Tavani, SAM–PCA3448. All × 1 unless otherwise stated.

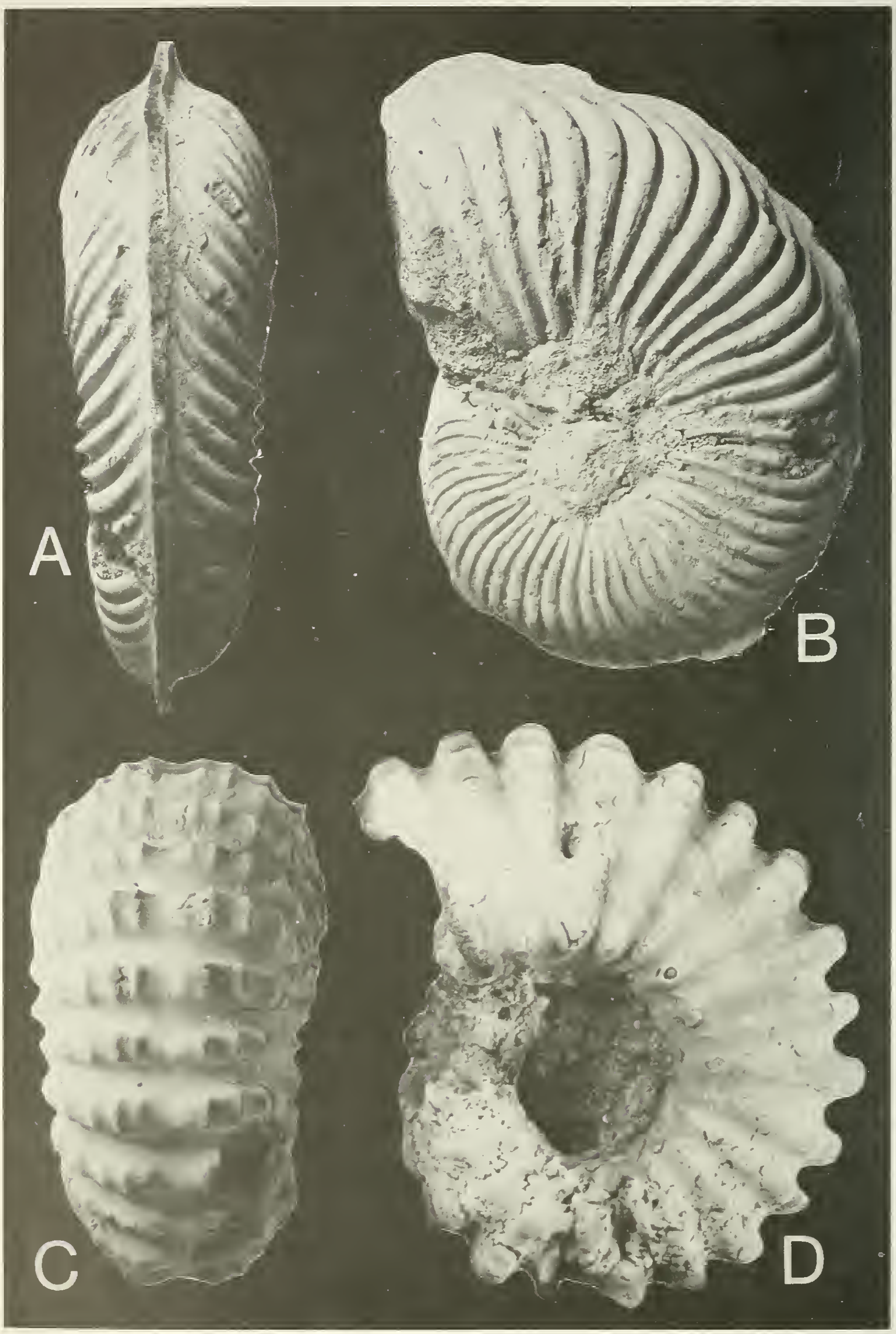

Fig. 5. A–B. *Oxytropidoceras (Oxytropidoceras) roissyanum* (d'Orbigny). The original of D'Orbigny's (1841) protograph, NHMP. C–D. *Douvilleiceras mammillatum mammillatum* (Schlotheim). The neotype, BM–C12491. Both × 1. Photos: W. J. Kennedy.

specimens the appearance of having had very much narrower ribs than, in fact, they probably had.

The shell is moderately evolute (umbilicus 32,5–39% of the diameter), with rather inflated whorls, and a subreniform depressed whorl section. In all the better preserved material the ventral sulcus is, or appears to have been, rather narrow. The number of notches to each rib varies with ontogeny, with about 5 at 30 mm diameter increasing to 8–9 at about 60 mm diameter. Up to about 40 mm diameter the ribs tend to be simple, distant and rursiradiate, commonly with 10–14 ribs per half whorl. However, several of the more densicostate juveniles have 16 ribs per half whorl. Beyond this diameter intercalation and bifurcation becomes increasingly common, generally with 16–20 rather uniform ribs per half whorl. One individual, SAM–PCA3417, retains simple ribbing to 62 mm diameter, whereas SAM–PCA3431 has very fine, nontuberculate intercalatories between main ribs at about 40 mm diameter, only to loose them with further growth. The tuberculation of this subspecies is very reduced, typically with the lateral tubercle subdued and bullate. In SAM–PCA3472, however, main ribs bear a prominent lateral tubercle and, up to 35 mm diameter, alternate with fine nontuberculate intercalatories. Beyond this diameter all the ribbing becomes uniform and the lateral tubercule is much reduced and bullate. In SAM–PCA3435, the early whorls are strongly tuberculate and distantly ribbed but, at 47 mm diameter, there is a sudden and dramatic reversion to normal *aequinodum*-type ornament. SAM–PCA3430 connects typical *aequinodum*-type morphologies to the large macroconch fragments (SAM–PCA3408, 3410–3411, 3414, 3425, 3433, 3465, 3483, 3500) in the collection.

Measurements

No	D	H	W	W/H	U
SAM–PCA3427	75	29	34	1,17	29 (39)
SAM–PCA3429	83	35	45	1,29	27 (32,5)
SAM–PCA3431	?	32	37	1,16	?
SAM–PCA3434	70	26	32	1,23	27 (38,5)
SAM–PCA3527	51	19	21	1,11	18 (35,3)

Discussion

Quenstedt (1849) described two species of *Douvilleiceras*, *D. aequinodum* and *D. inaequinodum*. Since the latter species is typically lower Middle Albian (Casey 1962), it may be reasonable to assume this is also the level of *D. aequinodum*. Such a supposition tends to be supported by their coexistence in the *eodentatus* Nodule Bed (Bed e of Destombes *et al.* 1977) (Fig. 12A–D, G–H) at Bully, Pays de Bray, France, and also in Angola. Since the Angolan *D. mammillatum* material is dominated by *aequinodum* morphotypes, with no undoubted individuals of *D. mammillatum* s.s. (Fig. 5C–D), it seems reasonable to assume that a genuine shift in population structure has occurred when

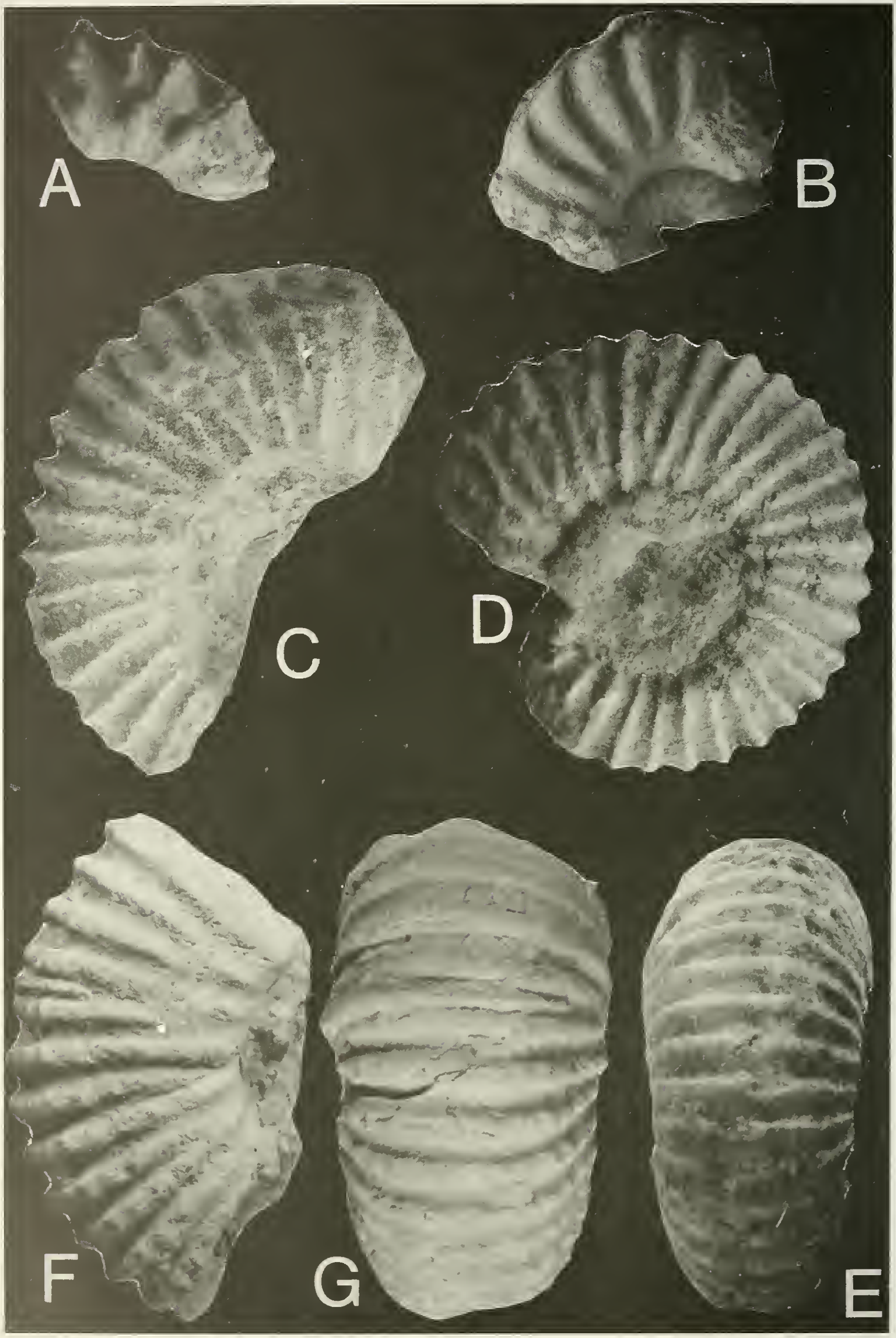

Fig. 6. A. *Douvilleiceras inaequinodum* (Quenstedt). SAM–PCA3535, a juvenile. B. *Oxytropidoceras (Mirapelia) buarquianum* (White), SAM–PCA3765, a typical juvenile. C–G. *Douvilleiceras mammillatum aequinodum* (Quenstedt). C. SAM–PCA3427. D–E. SAM–PCA2639. F–G. SAM–PCA3431. All × 1.

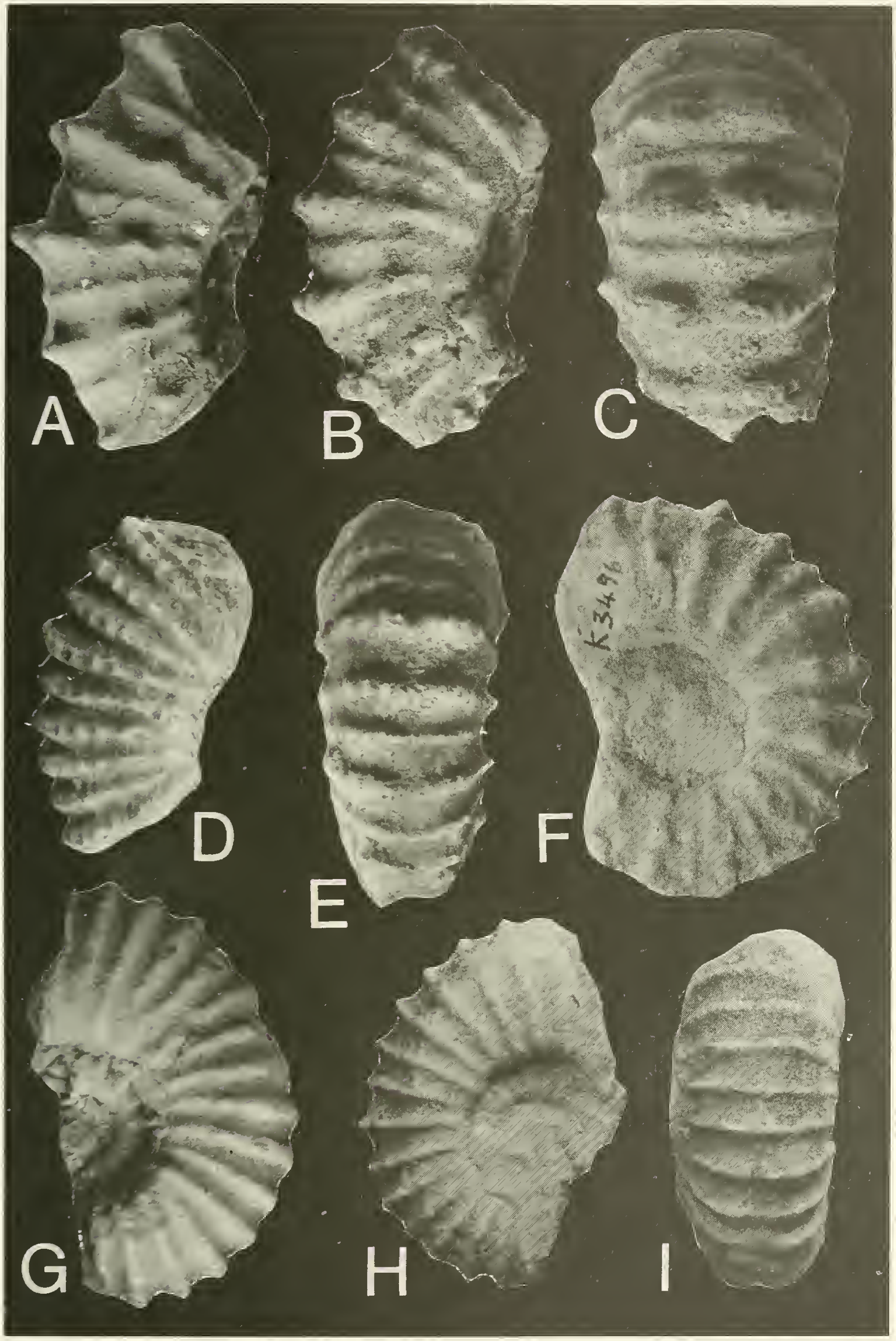

Fig. 7. A–C. *Douvilleiceras inaequinodum* (Quenstedt). A. SAM–PCA3466. B–C. SAM–PCA3437, a typical example. D, G–I. *Douvilleiceras mammillatum aequinodum* (Quenstedt). D. SAM–PCA3479. G. SAM–PCA3481. H–I. SAM–PCA3527, a typical juvenile with fine, distant, simple ribs. E–F. *Douvilleiceras variabile* Tavani, SAM–PCA3496. All × 1.

compared with the typical *mammillatum* Zone assemblages of *D. mammillatum* (cf. Casey 1962). It is for this reason, and because *D. aequinodum* can arguably be regarded as typically Middle Albian, that the writer has used Quenstedt's name at subspecific level. As noted by Casey (1962) *aequinodum* morphotypes are also abundant in the *mammillatum* Zone of England, but at this level coexist with, and are connected by transitions to, *D. mammillatum* s.s., *D. mammillatum* var. *praecox* Casey, and *D. monile* (J. Sowerby). Since there is, in the writer's opinion, but a single biological taxon involved in the latter list, the various nominal forms are merely morphotypes within a single polytypic species. Disregarding the nomenclatural problems, it is clear that the Angolan population of *D. mammillatum* is substantially different from that at Copt Point, Folkestone, and thus warrants subspecific distinction.

Both *Douvilleiceras restitutum* Anderson and *D. cheloniceratiforme* are based upon macroconchs whose inner whorls suggest they may belong here. Similarly, the hypotype of *D. spiniferum* (Whiteaves) figured by McLearn (1972, pl. 28 (fig. 1)) also shows few features to distinguish it from typical *aequinodum* morphotypes. In addition, one of White's (1887, pl. 23 (fig. 4)) syntypes of *D. offarcinatum* shows a rib density that suggests possible reference to Quenstedt's taxon.

Douvilleiceras variabile Tavani, 1949

Figs 4G, 7E–F, 8C–D, 9G, 11C–D, 13A, 15E, 22A

Ammonites mammillaris Schlotheim, d'Orbigny, 1841: 249, pl. 72 (fig. 5 only).
Douvilleiceras variabile Tavani, 1949: 37, pl. 10 (figs 1–2).
? *Douvilleiceras pseudinaequinodum* Collignon, 1963: 120, pl. 288 (fig. 1249).
Douvilleiceras monile (J. Sowerby) Collignon, 1963: 118, pl. 287 (fig. 1248).
Douvilleiceras aff. *baylei* Spath, Collignon, 1963: 118, pl. 287 (fig. 1247).
Douvilleiceras subleightonense Mirzoyev, 1967: 59, pl. 8 (figs 1–3).
? *Douvilleiceras* sp. B, McLearn, 1972: 67, pl. 13 (fig. 1), pl. 16 (fig. 1).

Material

Four specimens, SAM–PCA3422, 3447–3448 and 3496, all preserved as internal moulds.

Description

In shell form, this species is very similar to the last but with substantially different ornament. In the Angolan material, ornament comprises well-developed main ribs ornamented with a distinct umbilical tubercle, a pronounced mid-lateral tubercle and bullate ventral tubercles that weaken beyond about 45 mm diameter and are lost at about 60 mm diameter. At about this stage a small tubercle also appears between the umbilical and mid-lateral tubercle, and the ventral tubercles bear three notches. There are, therefore, eight notches per rib. Between these long ribs are invariably one, sometimes two intercalatories that do not connect with the umbilicus and lack mid-lateral tubercles. These ribs tend to be somewhat finer than the main ribs and give rise to the typical 'variable' ornament of this species.

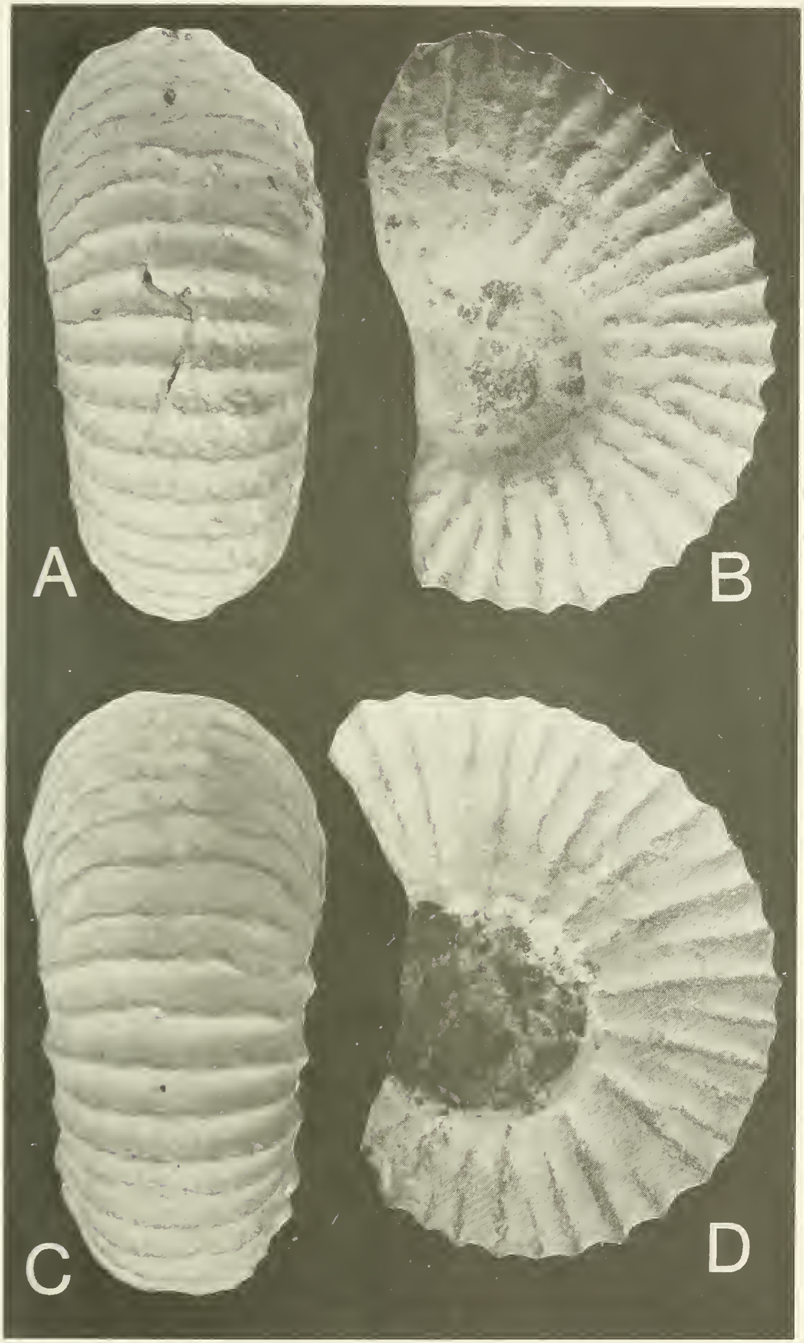

Fig. 8. A–B. *Douvilleiceras mammillatum aequinodum* (Quenstedt), SAM–PCA 3429. C–D. *Douvilleiceras variabile* Tavani, SAM–PCA3447. Note the alternating long and short ribs and prominent lateral tubercle typical of this species. Both × 1.

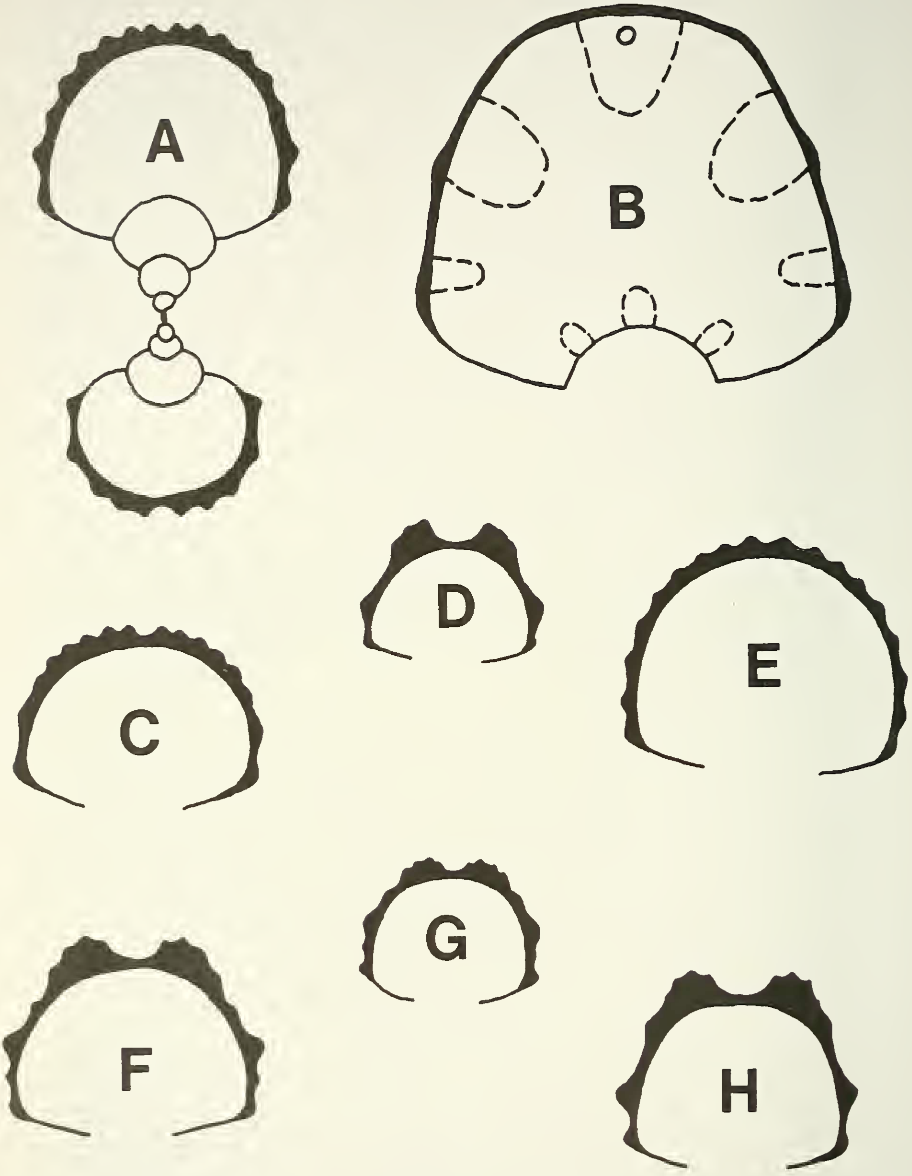

Fig. 9. Whorl sections of *Douvilleiceras*. A–C, E. *Douvilleiceras mammillatum aequinodum* (Quenstedt). A. SAM–PCA3417. B. SAM–PCA3433. C. SAM–PCA3479. E. SAM–PCA 3431. D, F, H. *Douvilleiceras inaequinodum* (Quenstedt). D. SAM–PCA3535. F. SAM–PCA3437. H. SAM–PCA 3466. G. *Douvilleiceras variabile* Tavani. SAM–PCA3496. All × 1.

Measurements

No	D	H	W	W/H	U
SAM–PCA3496	51	19	22	1,16	19 (37)

Discussion

Douvilleiceras variabile Tavani seems to be based upon the inner whorls of a macroconch, showing the irregular ornament of the early growth stages, with 1–2 weak ribs between main ribs, and the more regular ornament of the macroconch on the adoral half of the last whorl. Tavani's (1949) species is undoubtedly very close to *D. mammillatum* (Schlotheim), and D'Orbigny's (1841, pl. 72 (fig. 5)) *Ammonites mammillaris* seems to be a typical example of this species. Indeed, even in the present collection, several individuals seem to combine the characters of *D. variabile* and *D. mammillatum aequinodum* (Fig. 15E). This tends to suggest that *D. variabile* is merely another morphotype within a polytypic *D. mammillatum*. While this is the writer's belief, opposition to the gross 'lumping' that such synonymies would involve from one of the referee's of this paper has led to the adoption of a somewhat more cautious approach. *Douvilleiceras variabile* is here maintained as a distinct species because the writer does not believe in sympatric subspecies.

Douvilleiceras subleightonense Mirzoyev is a gigantic macroconch attaining some 600 mm diameter, whose inner whorls show the irregular ribbing typical of this species, and it may reasonably be included here. The *Douvilleiceras* sp. B of McLearn (1972, pl. 13 (fig. 1), pl. 26 (fig. 1)) is another macroconch that may belong here. Yet another macroconch whose inner whorls are reminiscent of this species is *D. pseudinaequinodum* Collignon. *Douvilleiceras ivernoisi* (Coquand) (Pictet & Renevier, 1854, pl. 2 (fig. 1)) is somewhat similar to *D. variabile*, but lacks the pronounced lateral tubercle.

Douvilleiceras inaequinodum (Quenstedt, 1849)

Figs 4C–D, F, 6A, 7A–C, 9D, F, H, 10E, 11A, 12C–D, G–H

Ammonites mammillaris Schlotheim, d'Orbigny, 1841: 249, pl. 73 (figs 1–3 only).
Ammonites monile inaequinodus Quenstedt, 1849: 138, pl. 10 (fig. 1).
Douvilleiceras inaequinodum (Quenstedt) Parona & Bonarelli, 1897: 95, pl. 4 (fig. 6), pl. 13 (fig. 6). Collignon, 1950: 46, fig. 2; 1963: 114, pl. 285 (fig. 1245). Casey, 1962: 282, fig. 95c.
Douvilleiceras orbignyi Hyatt, 1903: 110. Casey, 1962: 279, pl. 40 (figs 6–8), pl. 42 (figs. 12–13). Howarth, 1965: 345, pl. 1 (fig. 5).
Douvilleiceras mammillatum var. *baylei* Spath, 1923: 70, pl. 5 (fig. 4).
Douvilleiceras aff. *inaequinodum* (Quenstedt) Spath, 1923: 73, pl. 4 (fig. 5).
? *Douvilleiceras* cf. *inaequinodum* (Quenstedt) Scott, 1937: 35, pl. 6 (figs 3–4), fig. 1.
Douvilleiceras alternans Casey, 1962: 282, pl. 42 (fig. 1), fig. 1021.
? *Douvilleiceras magnodosum* Casey, 1962: 284, pl. 42 (fig. 4), fig. 102k.
? *Douvilleiceras charshangense* Mirzoyev, 1967: 54, pl. 7 (figs 1–5).
? *Douvilleiceras* sp. A, McLear, 1972: 67, pl. 12 (fig. 1).
Douvilleiceras cf. *orbignyi* Hyatt, Young, 1974: 188, pl. 5 (figs 9–10).

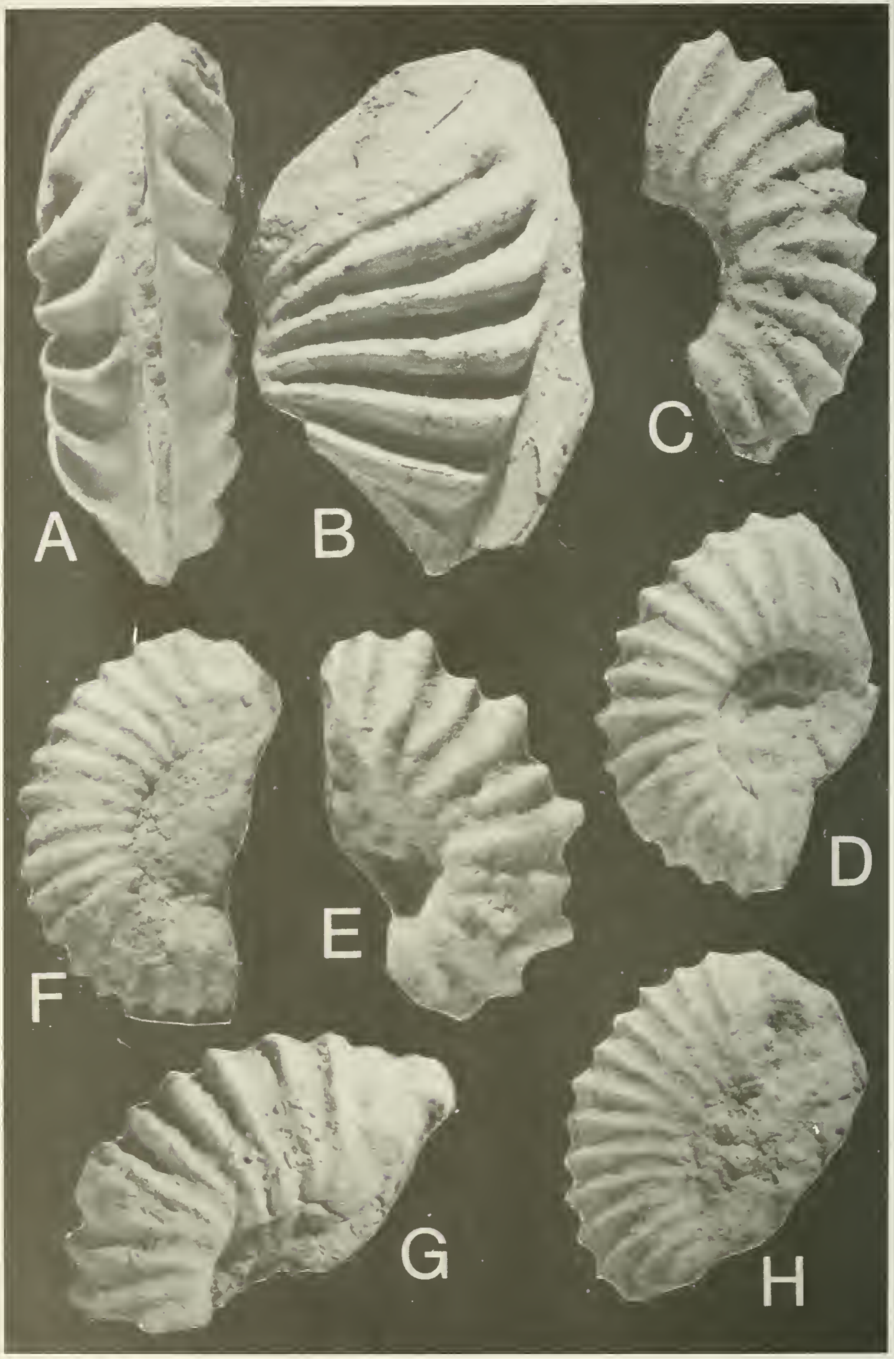

Fig. 10 A–B. *Oxytropidoceras (Mirapelia) buarquianum* (White). SAM–PCA2656. a *douglasi* morphotype which very closely approaches *O. mirapelianum* (d'Orbigny). × 0,75. C–D, F–H. *Douvilleiceras mammillatum aequinodum* (Quenstedt). C. SAM–PCA3494. D. SAM–PCA 3503. F. SAM–PCA3527. G. SAM–PCA3499. H. SAM–PCA3518. E. *Douvilleiceras inaequinodum* (Quenstedt), SAM–PCA3504. All × 1 unless otherwise stated.

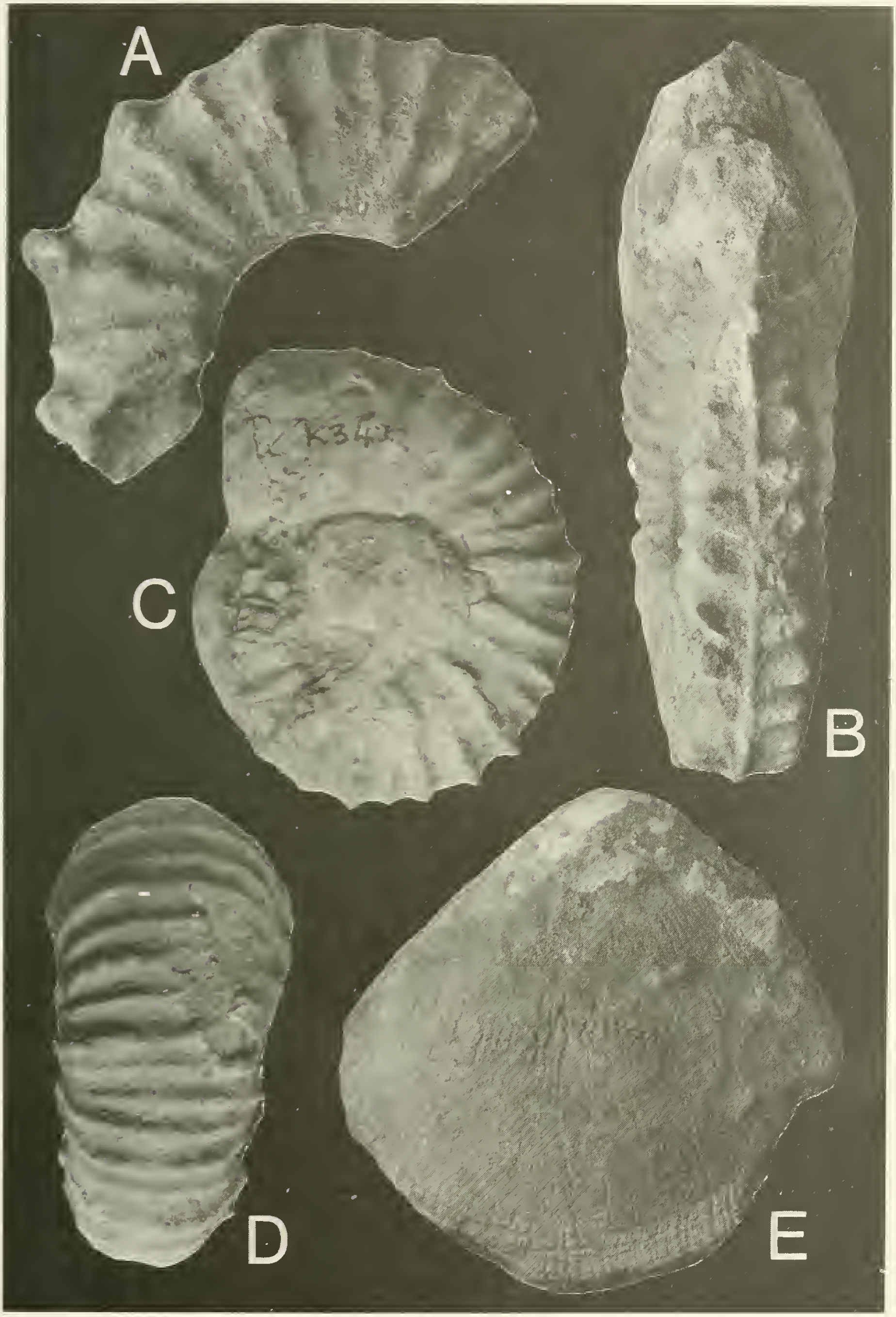

Fig. 11. A. *Douvilleiceras inaequinodum* (Quenstedt), SAM–PCA3458, a specimen showing the increased number of intercalatories in maturity. B. *Oxytropidoceras (Mirapelia) sergipense* (White). Front view of SAM–PCA5444. C–D. *Douvilleiceras variabile* Tavani, SAM–PCA3422. *E. Plagiostoma* sp., SAM–PCA5490, from the *Oxytropidoceras* assemblage. All × 1.

Material

Eighteen specimens, SAM–PCA3435–3438, 3444, 3451, 3453, 3456–3458, 3466, 3492, 3495, 3498, 3504, 3512, 3525, and 3535, all preserved as limestone steinkerns.

Description

This is a rather common species in the Angolan fauna. The shell is generally moderately evolute, inflated, with a subreniform, depressed whorl section. The umbilicus is rather wide, with steep umbilical walls and well-rounded shoulders. Ornament comprises sparse, distant, slightly rursiradiate ribs, which are narrower than the interspaces and alternate weak and strong. The strong main ribs are ornamented with small umbilical tubercles, a prominent lateral tubercle, and exaggerated ventral bulges, each with three spiral notches. In juveniles, only two spiral notches are present on the ventral bulges. With ontogeny, a small tubercle appears between the umbilical and mid-lateral tubercle and another between the latter and the ventrolateral bulges. Thus, there may be up to eight crenulations per rib in adults. The fine intercalated ribs, usually one and rarely two, between main ribs generally lack discernible ornament (on the weathered internal moulds), but in some individuals develop a small but distinct mid-lateral tubercle. In the early growth stages (Figs 4C–D, 12G–H) the intercalated ribs may be absent or so fine that there is difficulty in distinguishing this species from *D. mammillatum* s.s. There are probably about 7–8 main ribs per half whorl. The ventral sulcus is moderately broad and rather deep.

Discussion

Casey (1962) considered *D. inaequinodum* to be a typical Middle Albian species, distinguished from the earlier *D. orbignyi* Hyatt and *D. alternans* Casey in having two, not one, fine intercalatories between main ribs. However, material from the *Isohoplites eodentatus* nodule bed at Bully, Pays de Bray, France (Fig. 12C–D), shows that at least some individuals of *D. inaequinodum* have but a single fine intercalated rib between main ribs. In view of this, and because Casey (1962) has noted transitions between *D. alternans* and *D. orbignyi*, the latter two species are included in the synonymy of *D. inaequinodum*. Until the population structures of the *mammillatum* Zone assemblages are better known, it is perhaps prudent to retain *orbignyi* as a subspecies for these forms, as *D. inaequinodum orbignyi* Hyatt.

Family **Anisoceratidae** Hyatt, 1900

Genus *Protanisoceras* Spath, 1923

Type species *Hamites raulinianus* d'Orbigny, 1842; by original designation

Protanisoceras sp.

Fig. 13B

Material

A single fragment, SAM–PCA3461, preserved as a limestone steinkern from the *Douvilleiceras* assemblage.

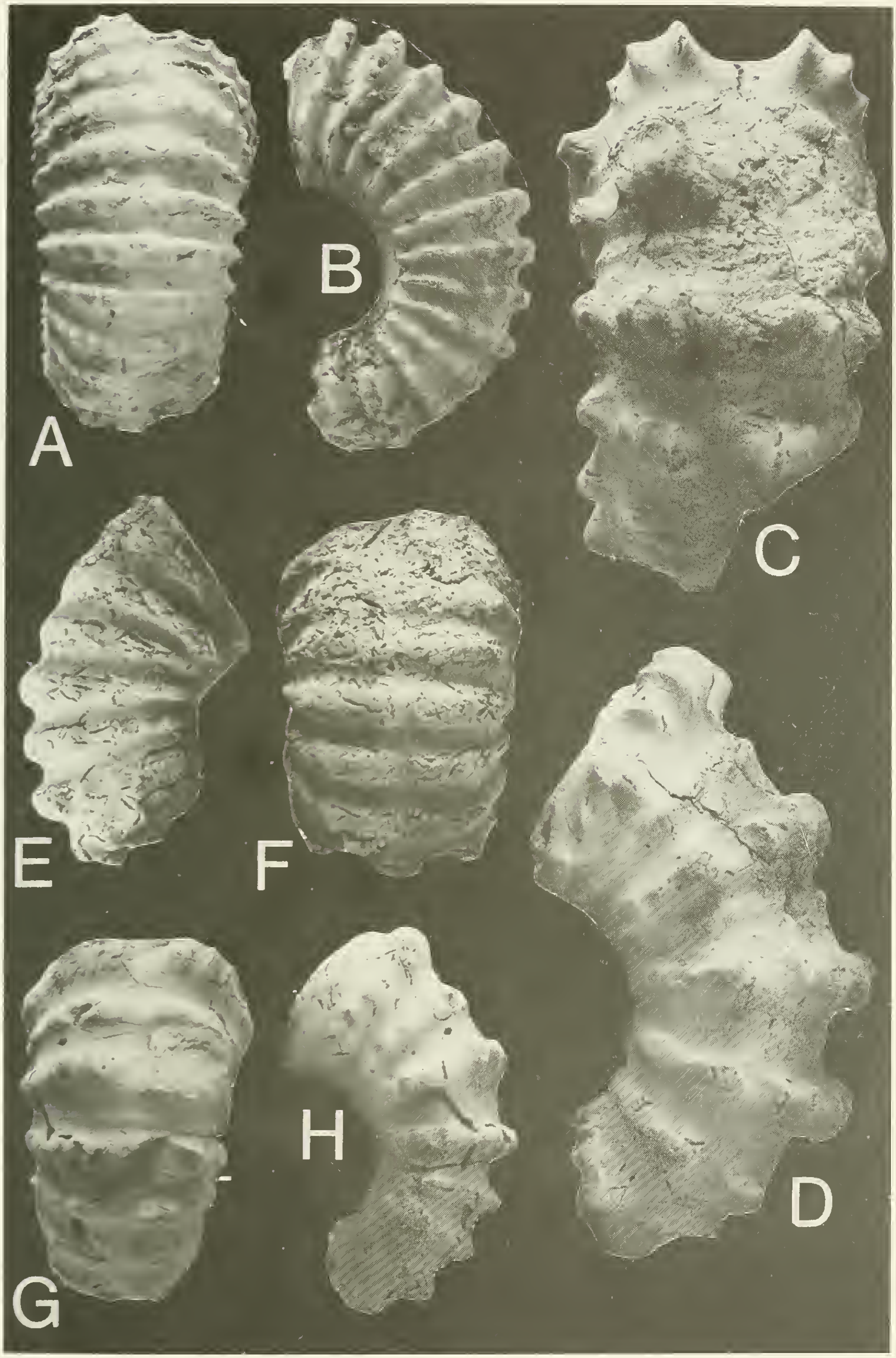

Fig. 12. *Douvilleiceras* spp. from the *I. eodentatus* Nodule Bed, Bully, Pays de Bray, France (Bed e of Destombes *et al.* 1977). A–B. *Douvilleiceras mammillatum aequinodum* (Quenstedt), OUM–KZ976. C–D, G–H. *Douvilleiceras inaequinodum* (Quenstedt). C–D. OUM–KZ982. G–H. OUM–KZ981. E–F. *Douvilleiceras mammillatum mammillatum* (Schlotheim), OUM–KZ979. All × 1.

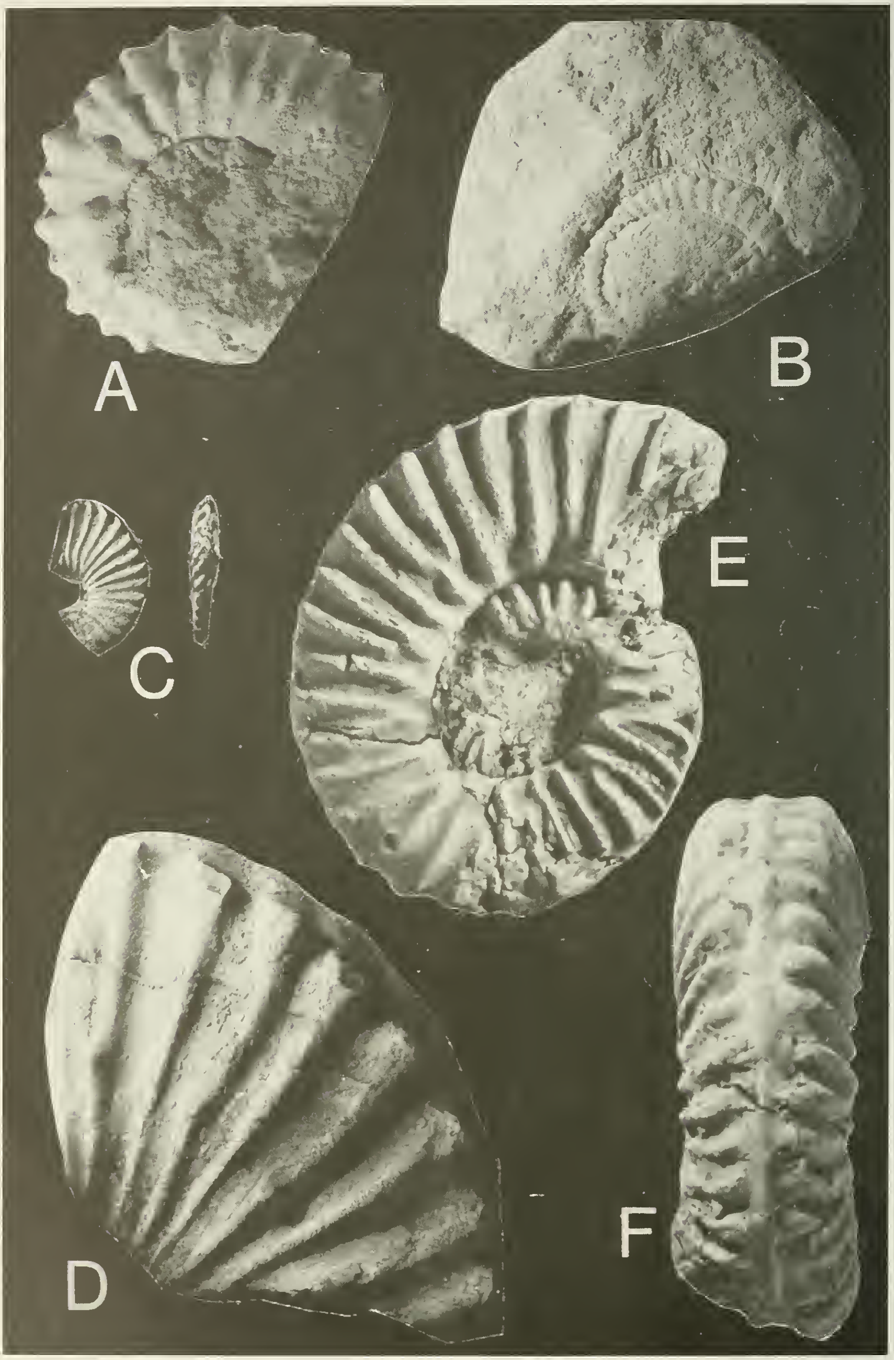

Fig. 13. A. *Douvilleiceras variabile* Tavani, SAM–PCA3472. B. *Protanisoceras* sp., SAM–PCA3461. C–D. *Venezoliceras acostae* (d'Orbigny), syntypes in the D'Orbigny Collection, NHMP. E–F. *Mortoniceratoides rigidus* (Spath), the holotype, BM–C34879. All × 1.

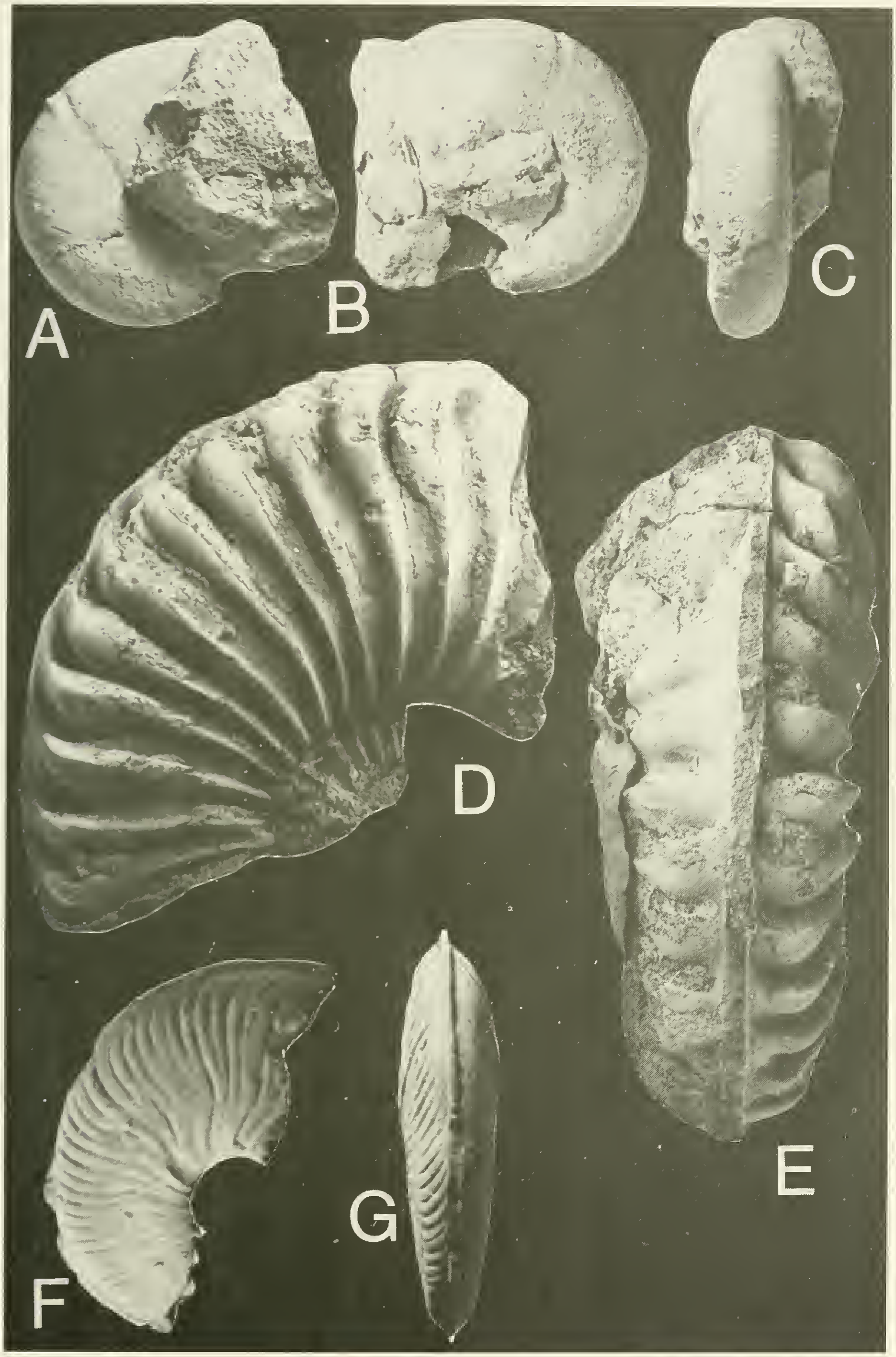

Fig. 14. A–C. *Puzosia bistricta* (White), the lectotype, designated herein, USNMNH 12102, from Porto dos Barcos, Mariom, Sergipe, Brazil. D–E. *Oxytropidoceras (Mirapelia) mirapelianum* (d'Orbigny), NHMP–5758, in the D'Orbigny Collection, from Clar, France. F–G. *Oxytropidoceras (Oxytropidoceras) carbonarium* (Gabb), the holotype of *O. cantianum* Spath, BM–C12501, from the *D. cristatum* Zone at Folkestone.

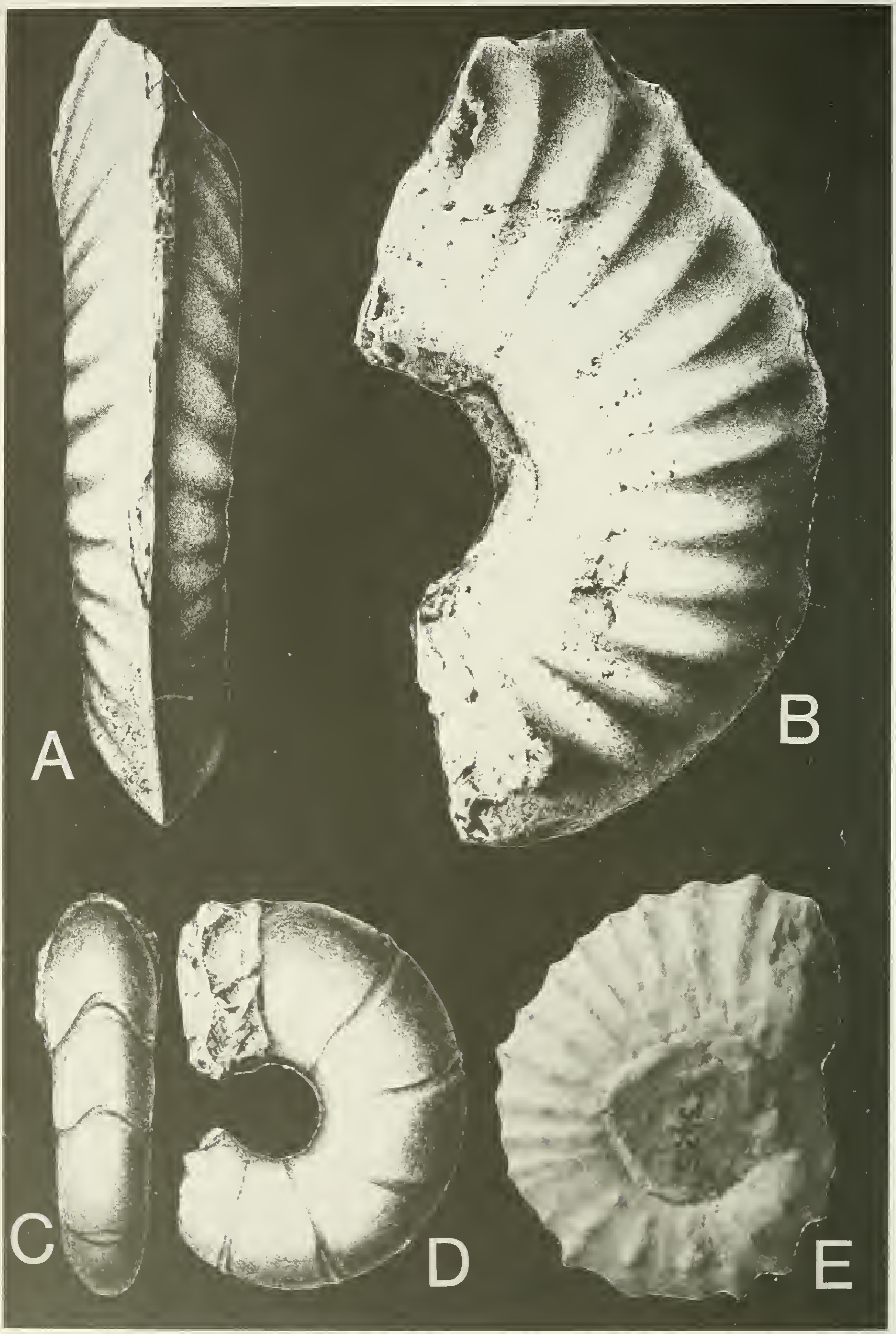

Fig. 15. A–B. *Oxytropidoceras (Mirapelia) buarquianum* (White), the lectotype, designated herein (after White 1887). C–D. *Puzosia bistricta* (White), copy of White's (1887) original illustration. E. *Douvilleiceras* cf. *variabile* Tavani, SAM–PCA3435. Note the abrupt change from a *variabile* to an *aequinodum*-type ornament. All × 1.

Description

The short curved fragment gives the impression of having had a compressed, elliptical whorl section. Ornament comprises rather broad, low, rursiradiate ribs, wider than the interspaces, each bearing a distinct ventrolateral tubercle. There are about three ribs in a distance equal to the whorl height.

Discussion

The available specimen is too fragmentary to warrant comparison with the many described species of *Protanisoceras*, but does provide the first record of this genus from Angola.

Family **Desmoceratidae** Zittel, 1895

Subfamily Puzosiinae Spath, 1922

Genus *Puzosia* Bayle, 1878

Type species *Ammonites mayoriana* d'Orbigny, 1842
(= replacement name for *A. planulatus* J. de C. Sowerby
non Schlotheim 1820 *nec* Schuebler 1830);
by subsequent designation

Puzosia bistricta (White, 1887)

Figs 2A–B, 3C–D, 14A–C, 15C–D, 16, 17B–C, 18C–D, 19A–B

Ammonites bistrictus White, 1887: 216, pl. 23 (figs 5–8).
Ammonites hopkinsi Forbes, White, 1887: 213, pl. 21 (figs 1–3), pl. 22 (fig. 5).
Puzosia welwitschia Choffat (*in* Choffat & de Loriol), 1888: 68, pl. 2 (fig. 4).
Puzosia garajauana Maury, 1930: 289; 1936: 234, pl. 20 (figs 1–3). Beurlen, 1970: 446, pl. 1 (figs 1–3), figs 1–2.
Puzosia rosarica Maury, 1936: 236, pl. 26 (figs 2–3). Beurlen, 1970: 446, pl. 1 (figs 4–5), figs 3–6.

Material

Thirty specimens, SAM–PCA2623, 2625–2626, 2636, 2638, 2649, 2652, 2660–2661, 3412, 3415–3416, 3419–3421, 3424, 3426, 3429, 3432, 3434, 3449, 3452, 3474–3475, 3635, 3749, 3751, 3753, 3757, all preserved as limestone steinkerns and mostly from the beds with *Douvilleiceras*.

Description

Shell moderately large, compressed, with a moderately narrow umbilicus (21–27% of the diameter). The umbilical walls are steep, with evenly rounded shoulders, and the flanks slightly convex, almost flat. Maximum width is just below mid-flank and the whorl section (Fig. 16) is elliptical. There are generally about 7–8 straight, prorsiradiate constrictions per whorl, which flex forward just before crossing the venter. Characteristically, the whorls show an increase in inflation immediately after a constriction. The constrictions are broad and shallow, typically with a peculiar wedge-shaped rib intercalated across the

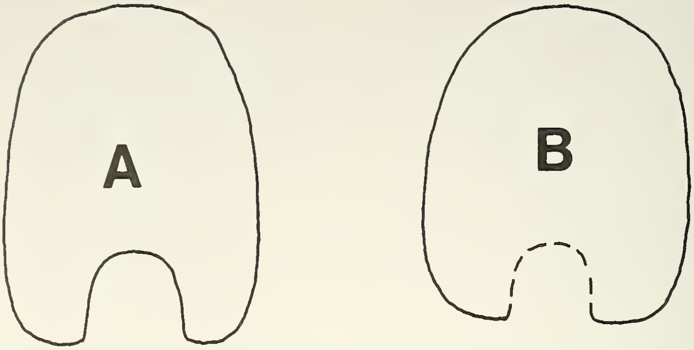

Fig. 16. Whorl sections of *Puzosia bistricta* (White). A. SAM–PCA2626. B. SAM–PCA3412. Both × 1.

venter in the middle growth stages. Because of the nature of preservation, the true characters of the ribbing are difficult to assess. They first appear on the outer parts of the flanks at about 60–80 mm diameter, and coarsen and become more prominent across the venter with age. On SAM–PCA2623 there are twenty fine ribs between successive constrictions whereas on SAM–PCA2649 there are only seven.

Discussion

Puzosia welwitschia Choffat is clearly conspecific with the *Ammonites hopkinsi* figured by White (1887), which was later renamed *Puzosia garajauana* by Maury (1930). They almost certainly merely represent the middle and adult growth stages, respectively, of *P. bistricta* (White) (Fig. 14A–C). *Puzosia rosarica* Maury occurs with *P. bistricta* and is based upon juvenile material which probably does not warrant specific separation. There are few species of *Puzosia* with which this highly distinctive Middle Albian species may be confused.

Family **Brancoceratidae** Spath, 1933

Subfamily Mojsisovicziinae Hyatt, 1903

Genus *Oxytropidoceras* Stieler, 1920

Type species *Ammonites roissyanus* d'Orbigny, 1841;
by original designation

Discussion

The most comprehensive treatment of this genus is that of Young (1966). He included *Androiavites* Collignon (1936) in the synonymy of *Adkinsites* and provided the following emended diagnosis of *Manuaniceras*: 'Ammonites with few whorls, which are much higher than wide; there are many flat ribs at some stage in the ontogeny, and ribs may be single or bifurcating at one or more positions at the umbilicus or on the flank' (p. 95).

Unfortunately, however, flat-topped ribs are not a feature of *Manuaniceras manuanense* (Spath) (Fig. 31B) and hence cannot be used in the formulation of a diagnosis of this taxon. As Young (1966) rightly pointed out, *Manuaniceras* is a direct descendant of the *Oxytropidoceras roissyanum* group, which mainly differs in showing rib bifurcation at various levels on the flank. The differences are slight and the writer finds little use for the genus/subgenus *Manuaniceras* which is here included in the synonymy of *Oxytropidoceras* s.s.

As noted by Young (1966), and is clear both from the stratigraphic record and described species of *Oxytropidoceras*, the history of this taxon is one of parallel evolution between two species groups. The *O. mirapelianum* (d'Orbigny) (Fig. 14D–E herein) plexus comprises *O. mirapelianum* (d'Orbigny), *O. evansi* (Spath), *O. douglasi* Knetchel, *O. buarquianum* (White), *O. sergipense* (White), *O. packardi* Anderson, *O. boulei* Collignon, *O. paucituberculatum* (Collignon), and *O. colcanapi* Collignon. These are all coarsely ribbed species without bifurcation or intercalation of the simple ribs. To this group the writer would assign the strongly derived species of *O. salasi* Young, *O. stenzeli* Young, and *O. pandalense* Young in which the adult whorls become densicostate, with occasional bifurcation and intercalation, and thus homoeomorph '*Manuaniceras*'. The other species group is that of *O. roissyanum* (d'Orbigny) in which the ribs are fine, with frequent bifurcation at or above the umbilical edge, and which includes all the described '*Manuaniceras*' species of Young (1966). Since these two plexi appear almost simultaneously at the base of the Middle Albian (Owen 1971) and evolved in parallel until their final extinction in the early late Albian, the writer believes they merit subgeneric distinction. The writer proposes, therefore, the new subgenus ***Oxytropidoceras (Mirapelia)*** to include all those coarse-ribbed species assigned to the *mirapelianum* plexus above, with *Ammonites mirapelianus* d'Orbigny as type species. *Oxytropidoceras (Mirapelia) sergipense* (White) provides the rootstock from which the typical coarse-ribbed species of *Venezoliceras* (of which *Tarfayites* Collignon (1966) is a synonym), such as *V. venezolanum* (Stieler), *V. acostae* (d'Orbigny) (Fig. 13C–D), *V. heueri* Young, *V. obscurum* Young, *V. texanum* Young, *V? chihuahuaense* (Böse), *V. kiowanum* (Twenhofel), *V. umsinenense* (Van Hoepen), *V. bituberculatum* (Collignon), *V. madagascariense* (Collignon), *V. robustum* (Renz) and *V. clavicostatum* (Renz), are derived. However, as noted by Young (1966) and Renz (1968), there is a second group of *Venezoliceras*, typified by *Venezoliceras harrisoni* Benavides-Cáceres, in which the early and middle growth stages show dense, bifurcating, nontuberculate ribbing, with a flank tubercle developed only at relatively large diameters. This group, which also includes *V. acutocarinatum* (Shumard), *V. multicostatum* (Renz), *V. intermedium* (Renz), and *V. karsteni* (Stieler), seems to have its ancestry in '*Manuaniceras*' and, as such, its similar-

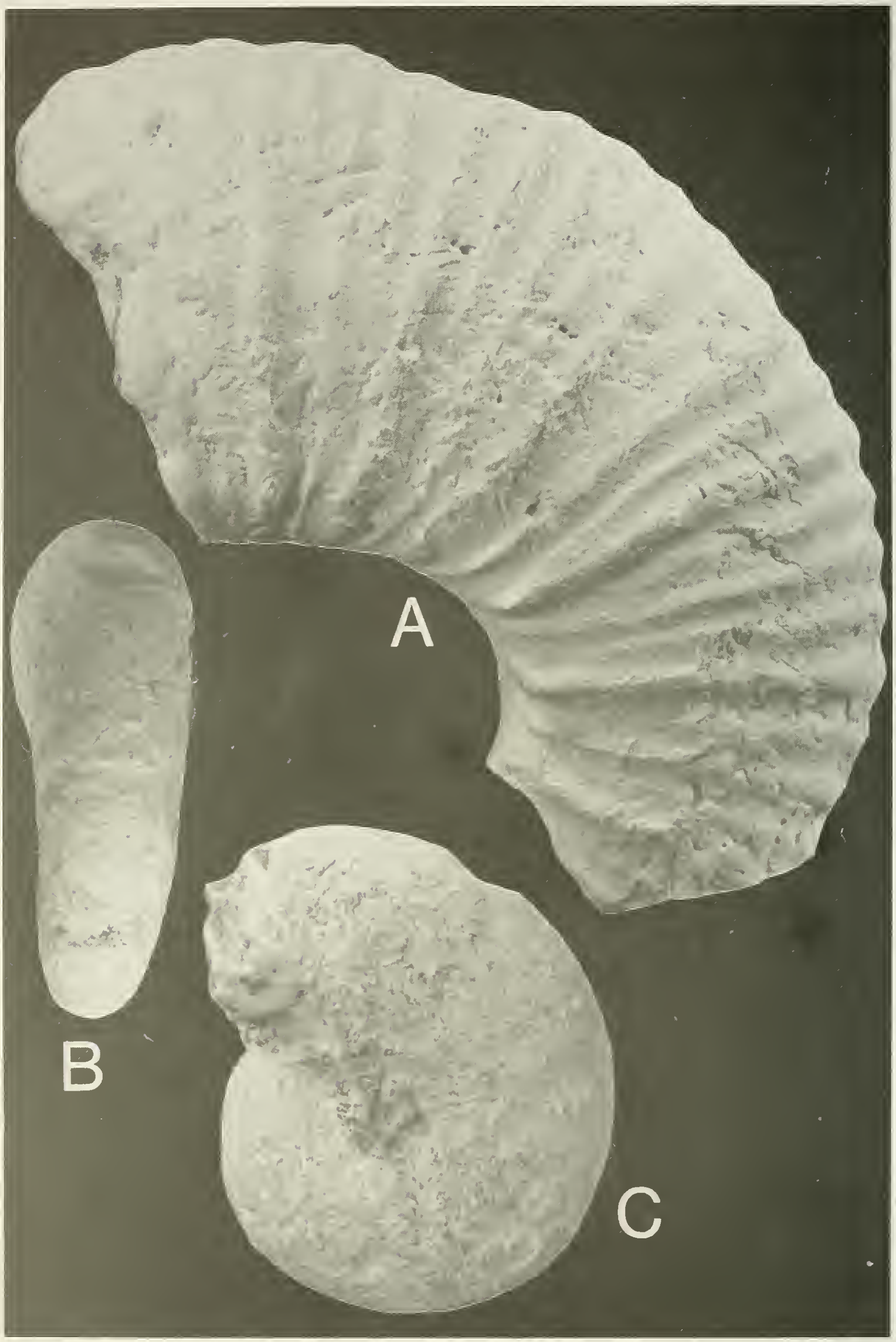

Fig. 17. A. *Douvilleiceras mammillatum aequinodum* (Quenstedt), SAM–PCA3423, a macroconch fragment, × 0,67. B–C. *Puzosia bistricta* (White), SAM–PCA5447, × 1.

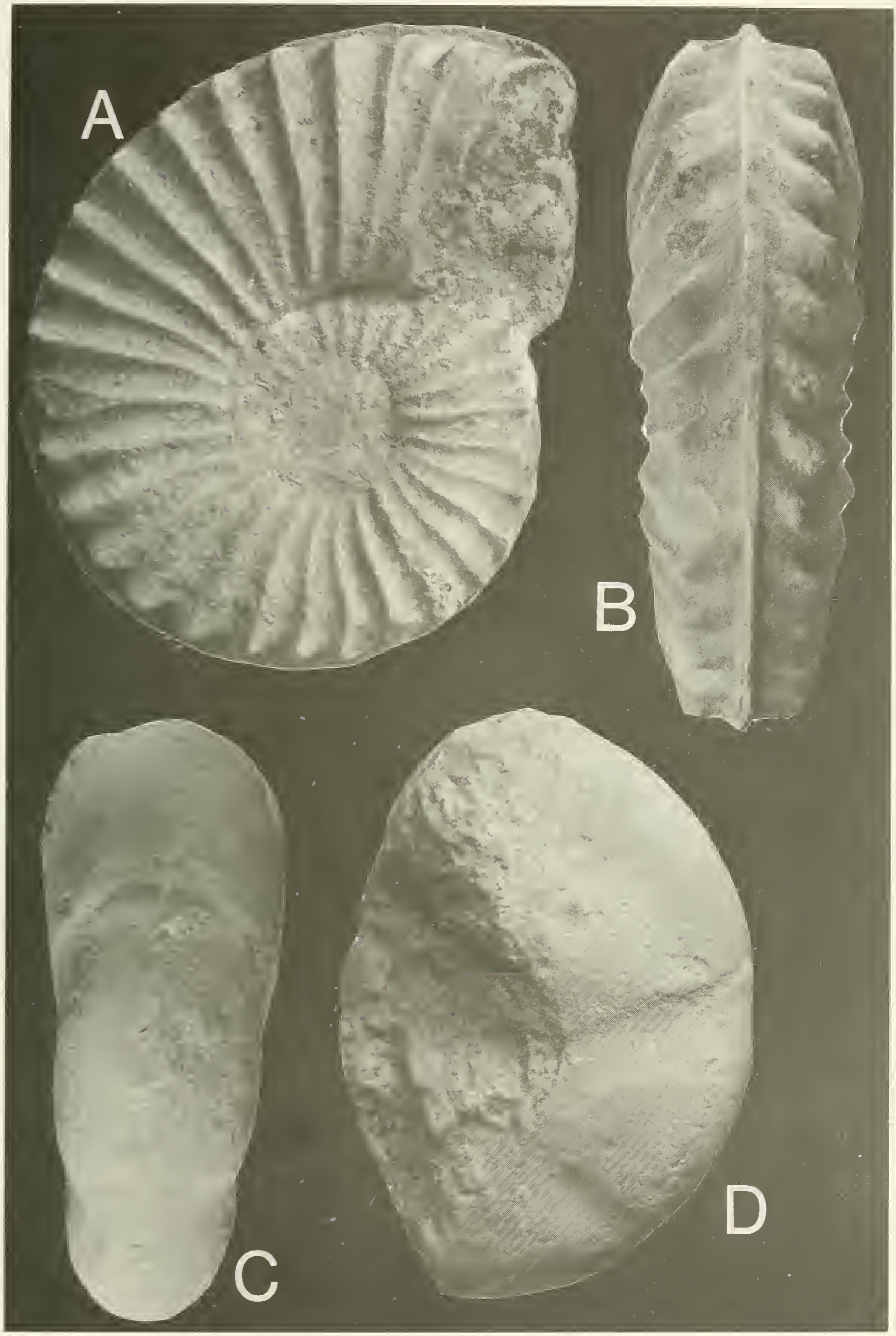

Fig. 18. A–B. *Oxytropidoceras (Mirapelia) sergipense* (White), SAM–PCA5444. C–D. *Puzosia bistricta* (White), SAM–PCA3420. Both × 1.

Fig. 19. A–B. *Puzosia bistricta* (White), a specimen in the South African Museum. C–E. *Oxytropidoceras (Mirapelia) buarquianum* (White). C. SAM–PCA5446, a *douglasi* morphotype. D–E. SAM–PCA3603, a *salasi* morphotype. All × 1.

ity to the *V. acostae* group is due to convergence. Consequently, the writer proposes the new subgenus ***Oxytropidoceras (Benavidesites)*****,** with type species *Venezoliceras harrisoni* Benavides-Cáceres (1956: 460, pl. 53 (fig. 6)), for this homoeomorphic development.

The origins of *Adkinsites* are obscure; Young (1966) would derive this taxon from *Dipoloceras*, but this view is unacceptable to the writer. They could represent derivatives of the more densely ribbed *O. (Mirapelia)* species or of paucicostate *Oxytropidoceras* s.s., or of both. This taxon is not present in the Angolan material and hence the writer defers judgement. Because of its obscure, and perhaps polyphyletic origins, Young (1966) is followed in treating *Adkinsites* as a genus, of which *Androiavites* Collignon (1936) is a synonym.

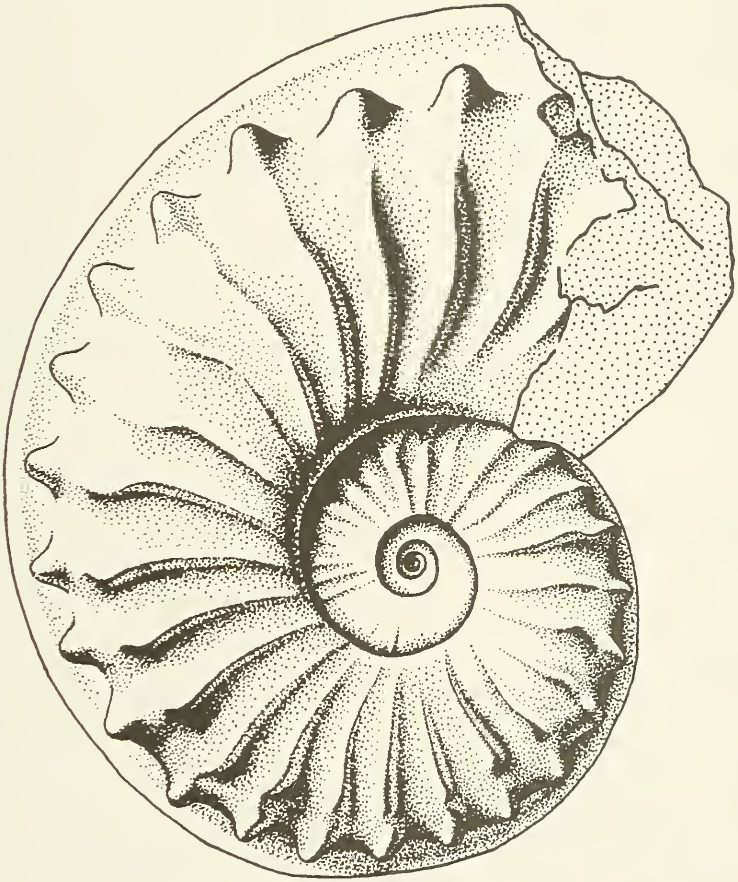

Fig. 20. *Mojsisoviczia* cf. *ventanillensis* (Gabb). A reconstruction based upon BM–C78865, from the Middle Albian of Zululand. × 1.

Mortoniceras (Pervinquieria) rigidum Spath (1933: 413, figs 142, 144f) (Fig. 13E–F herein) is recorded from Bed VIII (= *D. cristatum* Zone) at Folkestone and is, as such, the earliest described species of *Mortoniceras*. It differs from the latter genus, however, in having rather fine, distant ribs with a steep adoral surface and a sloping adapical surface, lacking any sign of a mid-lateral tubercle, and in lacking the doubling of the ventrolateral tubercle so typical of *Mortoniceras*. Indeed, the characters of ornament ally *M. rigidum* with the Mojsisovicziinae and it seems likely that *M. rigidum* is closely allied to, and perhaps descended from *Adkinsites*. Since the origins of *Mortoniceras* are generally thought to lie in *Dipoloceras* (Wright *in* Arkell *et al.* 1957), the similarities are due to convergence. It is proposed, therefore, to make *M. rigidum* Spath the type species for the new genus ***Mortoniceratoides***. It differs from *Adkinsites* in having a subquadrate whorl section, low ventral keel, and with a symmetrically bifid first lateral saddle.

As discussed by Kennedy & Cooper (1977), *Mojsisoviczia* and *Falloticeras* are closely allied and, on the basis of the available evidence, *Falloticeras* may reasonably be considered a neotonous offshoot of *Mojsisoviczia*. From their first appearance (Fig. 20), the ribs of *Mojsisoviczia* are coarse and simple and the origins of this taxon seem to lie in *O. (Mirapelia) sergipense* (White) or a closely allied form.

Dipoloceras is believed by Spath (1931) to have descended from *Oxytropidoceras*, and is included in the Mojsisovicziinae by Wright (*in* Arkell *et al.* 1957). However, the inflated whorls, low ventral keel and strong spiral ornament suggest a closer relationship with the Mortoniceratinae, to which subfamily *Dipoloceras* is here referred. The suggested phylogeny within the Mojsisovicziinae, as here interpreted, is shown as Figure 21.

Oxytropidoceras (Mirapelia) buarquianum (White, 1887)

Figs 3A–B, 6B, 10A–B, 15A–B, 19C–E, 22D–E, 23A–D, F–G, 24–25, 27

Ammonites buarquianus White, 1887: 222, pl. 24 (figs 3–4 only), pl. 25 (figs 7–8).
Schloenbachia cf. *roissyana* (d'Orbigny) Douvillé, 1906: 147, pl. 4 (fig. 3).
Schloenbachia aff. *belknapi* (Marcou) Douvillé, 1906: 148, pl. 2 (fig. 4).
Schloenbachia cf. *belknapi* Böse (*non* Marcou) Douglas, 1921: 269, pl. 17 (figs 1–2).
Schloenbachia cf. *chihuahuaensis* Böse. Douglas, 1921: 269, pl. 17 (fig. 3).
Oxytropidoceras buarquianum (White) Maury, 1936. pl. 19 (figs 2–3), pl. 25 (figs 5–6). Oliveira & Leonardos. 1943, pl. 27 (fig. 7). Young. 1966: 89. pl. 38 (figs 1–3). Beurlen, 1970: 464. pl. 5 (figs 1–2), fig. 18.
? *Oxytropidoceras colcanapi* Collignon. 1936: 182, pl. 18 (fig. 7), fig. 12k.
? *Oxytropidoceras* sp.juv., Spath, 1930: 61, pl. 9 (fig. 18).
Oxytropidoceras packardi Anderson, 1938: 198, pl. 50 (fig. 1).
Oxytropidoceras douglasi Knetchel, 1947: 106, pl. 24 (figs 1–4), pl. 25 (figs 1–2), pl. 26, pl. 27 (figs 2–3). pl. 28 (fig. 1). Young, 1966: 88, pl. 10 (figs 1, 5), pl. 36 (figs 3–4), pl. 37 (figs 4–5).
? *Oxytropidoceras involutum* Beurlen. 1952: 162, fig. 3.
? *Oxytropidoceras (Manuaniceras) involutum* Beurlen, 1970: 465, pl. 5 (fig. 4).
Oxytropidoceras sp. A, Beurlen, 1970: 464. pl. 5 (fig. 3).

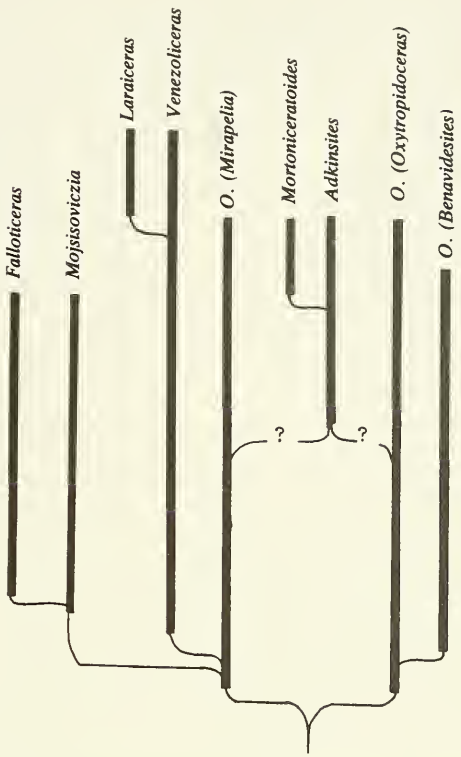

Fig. 21. A suggested phylogeny of the Mojsisovicziinae.

Material

Forty-five specimens, including SAM–PCA2617–2618, 2621–2622, 2627–2630, 2632, 2637, 2640–2645, 2648, 2651, 2654, 2659, 2663, 2665–2667, 2669, 2673–2674, 2676, 2678, 2693, 3603–3604, 3755, 3762 and 3765, all preserved as limestone steinkerns.

Description

The Angolan population is polytypic, with morphotypes agreeing exactly with *O. buarquianum* (White), *O. packardi* Anderson, *O. douglasi* Knetchel, *O. salasi* Young, and two specimens very closely approaching *O. mirapelianum* (d'Orbigny). The relationship between these morphotypes is shown in Figure 26. Because of this wide range of intraspecific variation, no single description will fully cover all morphotypes and hence they are described separately.

Two specimens, SAM–PCA2656–2657, very closely approach *O. mirapelianum* (d'Orbigny) and, with a typological approach, would be referred to that species. The Angolan examples (Fig. 10A–B) are, however, insensibly con-

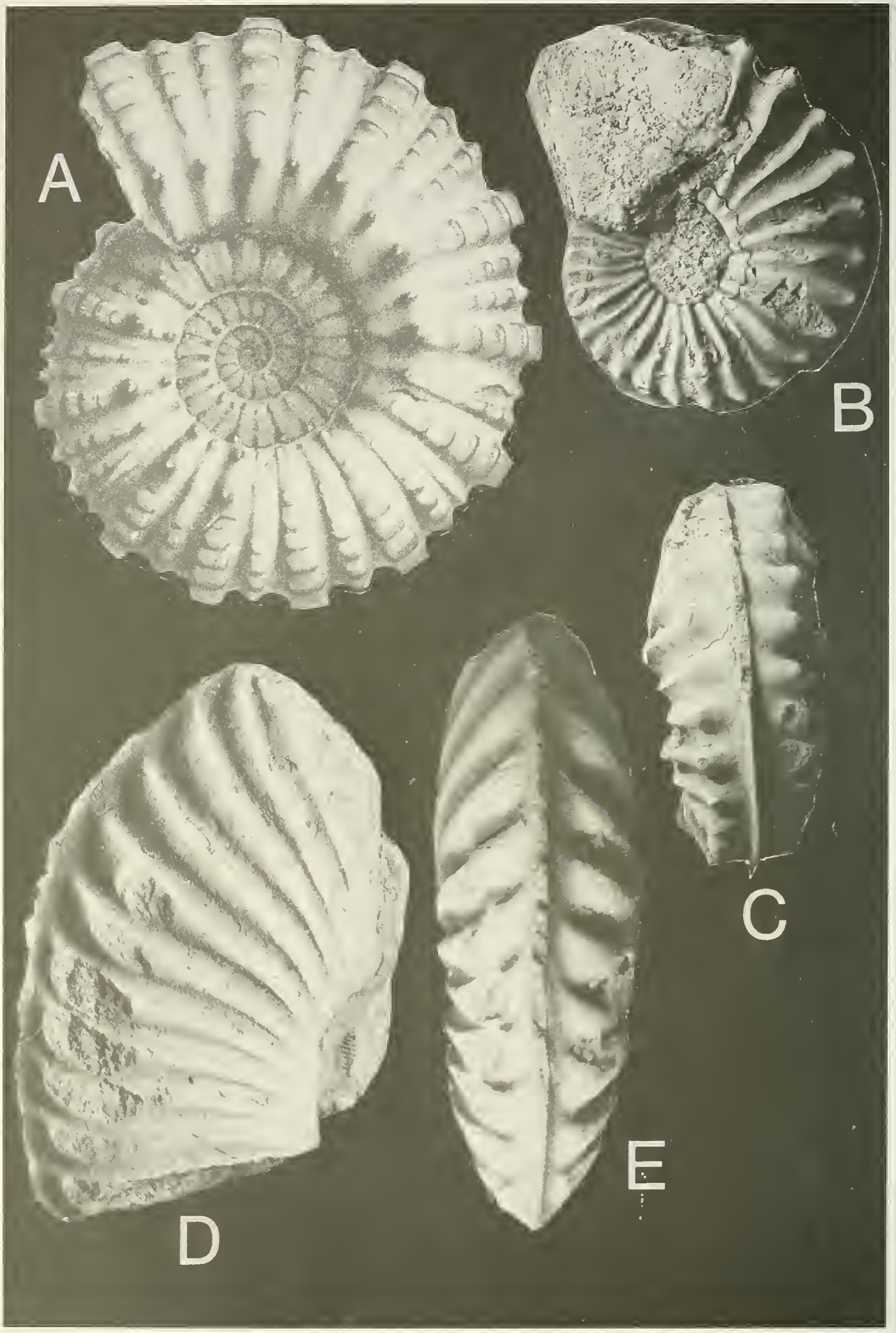

Fig. 22. A. *Douvilleiceras variabile* Tavani, D'Orbigny's (1841, pl. 72 (fig. 5)) protograph, × 0,5. B–C. *Mojsisoviczia delaruei* (d'Orbigny), NHMP–5761, one of D'Orbigny's syntypes from Clar, France. D–E. *Oxytropidoceras (Mirapelia) buarquianum* (White), SAM–PCA2641, a rather densely ribbed *douglasi* morphotype, thus transitional to *salasi* variants. All × 1 unless otherwise stated.

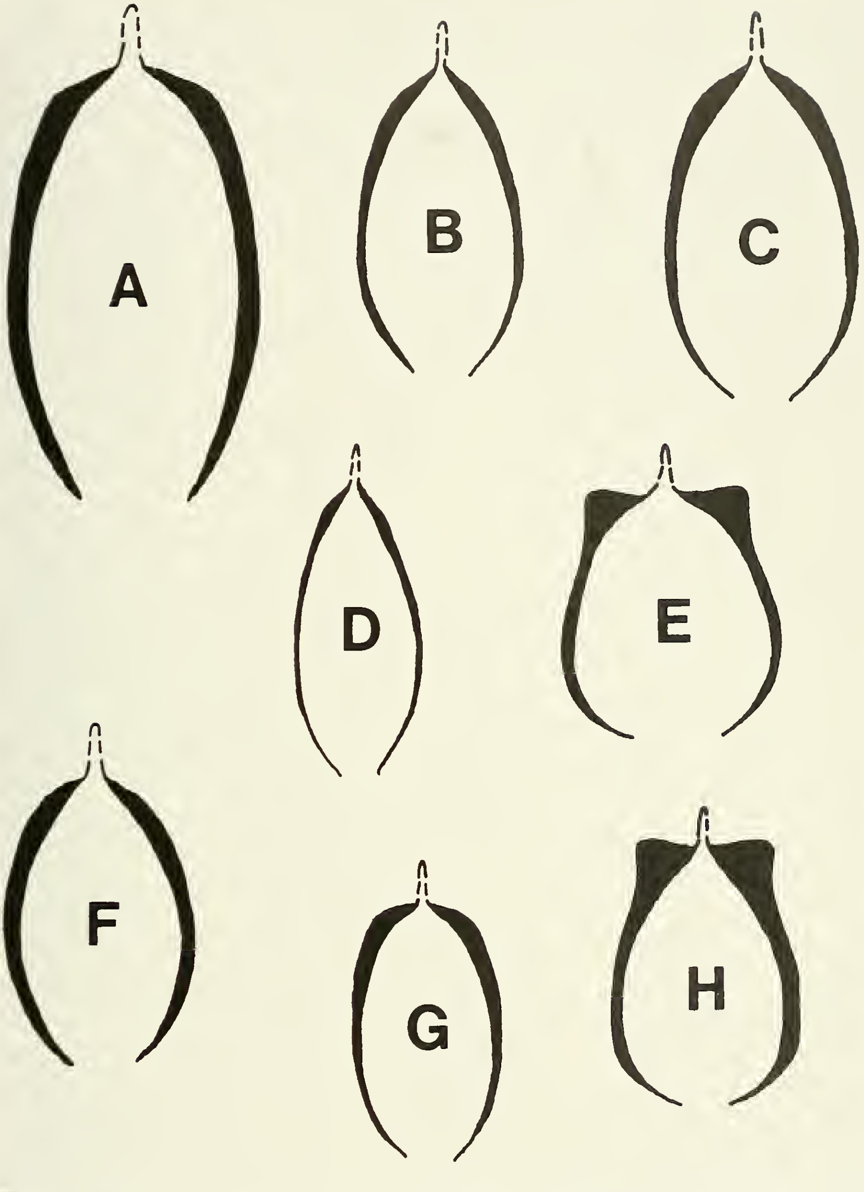

Fig. 23. A–D, F–G. Whorl sections of *Oxytropidoceras (Mirapelia) buarquianum* (White). A. SAM–PCA2656, a *douglasi* morphotype. B. SAM–PCA2644, a *douglasi* morphotype. C. SAM–PCA3603, a *salasi* morphotype. D. SAM–PCA2693, a typical *buarquianum* morphotype. F. SAM–PCA2622, a *douglasi* morphotype. G. SAM–PCA2641, a *douglasi* morphotype. E, H. Whorl sections of *O. (M.) sergipense* (White). E. SAM–PCA5444. H. An unnumbered specimen in the South African Museum. All × 1.

Fig. 24. *Oxytropidoceras (Mirapelia) buarquianum* (White), SAM–PCA3418, a *douglasi* morphotype, × 1.

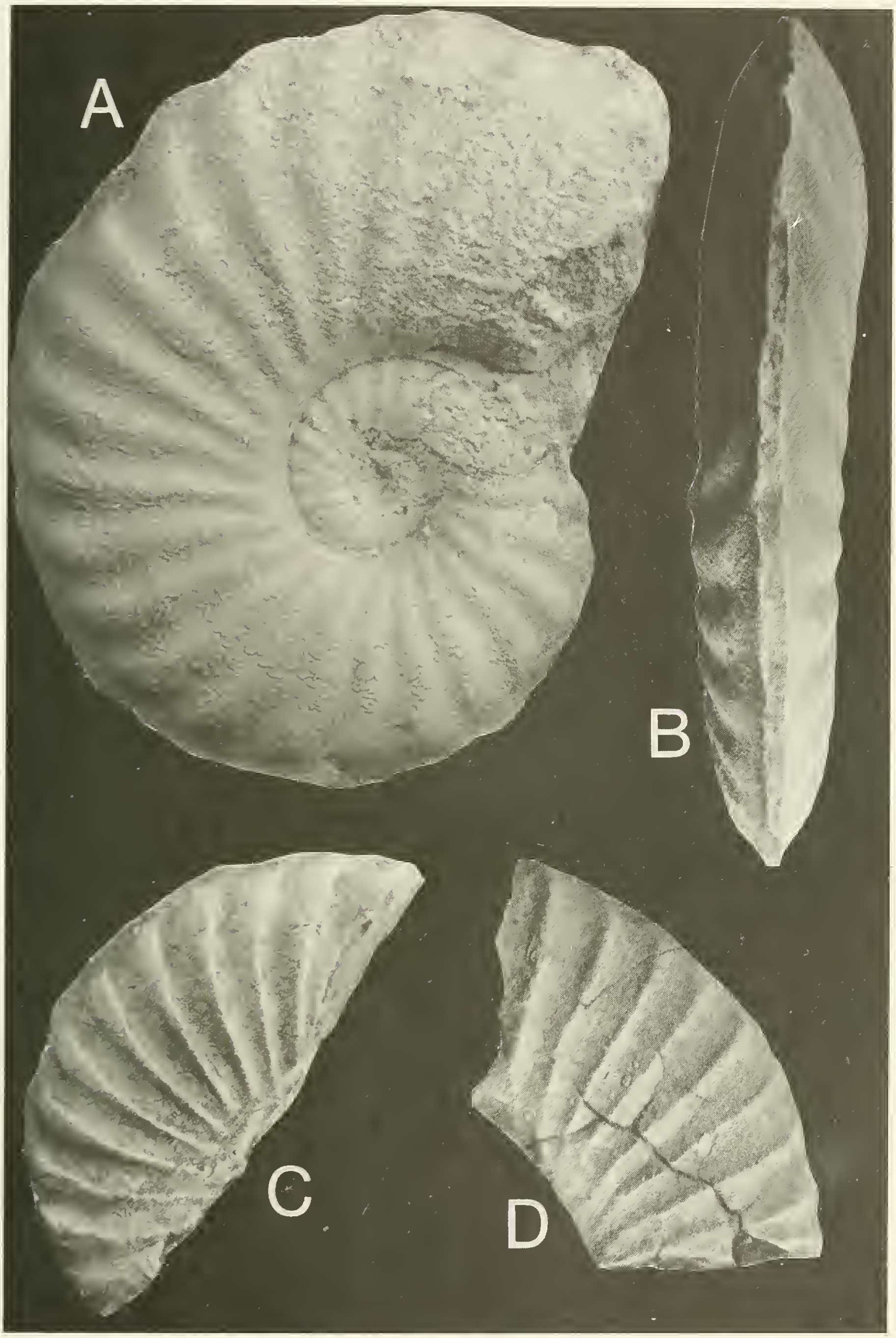

Fig. 25. *Oxytropidoceras (Mirapelia) buarquianum* (White). A–B. SAM–PCA2693, the typical variant. C. SAM–PCA2674, a *douglasi* morphotype. D. SAM–PCA2665, a rather eroded, finely ribbed variant. All × 1.

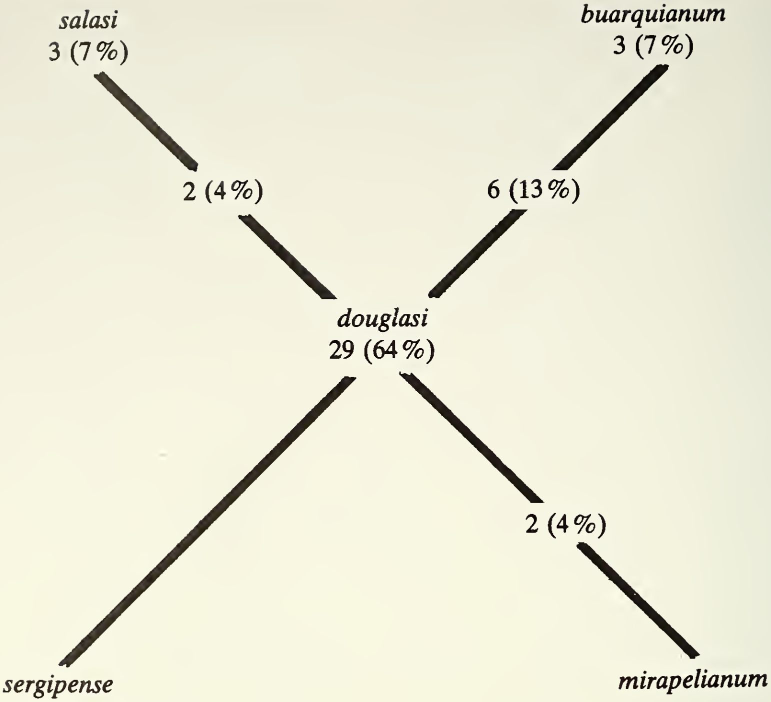

Fig. 26. Interrelationships between the *Oxytropidoceras (Mirapelia) buarquianum* morphotypes and closely allied species. Figures given are the number of morphotypes in the present collection followed, in parentheses, by the percentage which they constitute.

nected to *O. douglasi* morphotypes and differ from D'Orbigny's (1841) species (Fig. 14D–E) in being slightly less inflated and in having the ribs somewhat thicker at the umbilical margin.

The *O. douglasi* morphotypes are the most abundant in the present collection and show the following features: shell compressed, evolute (umbilicus 24–28% of the diameter), with a compressed, lanceolate whorl section and a prominent, sharp, high, siphonal keel. The umbilicus is rather wide and shallow, with fairly steep umbilical walls and evenly rounded shoulders at moderate diameters. The umbilical walls become increasingly inclined with growth and, in maturity, the umbilical shoulder is gently rounded and indistinct. At this stage, the outer whorl covers about 15 per cent of the ribbing of the preceding whorl. Maximum width is slightly below mid-flank in most individuals. Ornament comprises simple, generally flexuous ribs, which arise at the umbilical seam but only become prominent on the flanks. All ribs are slightly prorsiradiate, steepest adorally and convex adapically, and broaden towards the ventrolateral shoulders where they swell but do not form tubercles.

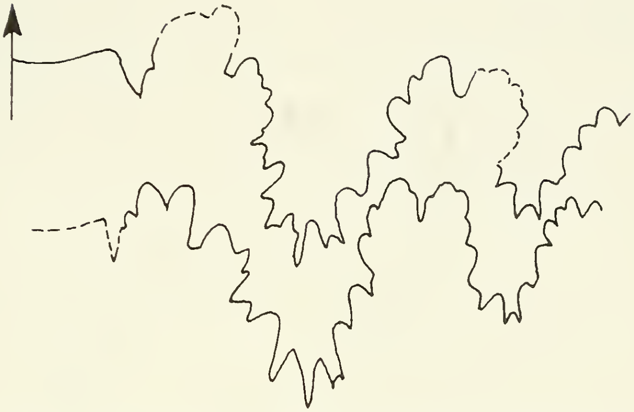

Fig. 27. *Oxytropidoceras (Mirapelia) buarquianum* (White). The suture line, somewhat simplified by erosion, of SAM–PCA2693, a *douglasi* morphotype. Approx. × 2.

There are 13–20 ribs per half whorl. A somewhat eroded suture-line is shown as Figure 27.

O. buarquianum morphotypes are insensibly connected to *O. douglasi* morphotypes (Fig. 3A–B). Typically (Fig. 25A–B), this morphotype is strongly compressed, with 22–32 broad, low, weak ribs per whorl, and an indistinct umbilical wall. It is perhaps worth noting that it is a 'law' of polytypic ammonite species that the compressed variants are weakly ornamented, and that strength of ornament increases with inflation.

Two examples, SAM–PCA 3603–3604, show the rather dense, straight ribs of *O. salasi* Young, becoming projected near the venter (Fig. 19D–E), and are connected by intermediates to *O. douglasi*. These *O. salasi* variants show a low umbilical wall, broad convex flanks and a lanceolate whorl section, and were clearly rather evolute. Although the siphonal keel is not preserved, it certainly stood well above the venter. The dense, narrow, simple ribs are distinctly prorsiradiate and only very slightly flexuous, with at least twenty-two ribs per half whorl. The ribs swell slightly at the ventrolateral shoulders and curve strongly forward to meet the siphonal keel.

Discussion

The Angolan material shows an insensible transition between *O. buarquianum* (White) and *O. douglasi* Knetchel and they are synonyms. It is unfortunate that White's (1887) species has priority because the *O. douglasi* morphotypes predominate. There is little to separate *O. packardi* Anderson from the *O. douglasi* morphotypes and it should also fall into synonymy. Several of the Angolan morphotypes are extremely close to *O. mirapelianum*, which is a broadly contemporaneous European species. However, until the population structure of D'Orbigny's (1841) species is better understood, they are maintained as specifically distinct.

As already noted, there are *O. salasi* morphotypes within the Angolan material, which are connected by transitions to *O. douglasi* morphotypes, but they constitute only 4 per cent of the present material. Because of this, and because Young (1966) had over 300 specimens of *O. salasi* from the Key Valley Marl, the Texas form is maintained as a distinct species. Occasional *O. salasi* morphotypes within the Angolan population merely indicate that *O. salasi* is descended from an *O. buarquianum* ancestor by a major change in population structure. *Oxytropidoceras stenzeli* Young (1966: 93, pl. 22 (fig. 1), pl. 26 (fig. 1), pl. 34 (fig. 1), pl. 35 (fig. 4), figs 7h, 18c) is a Middle to low Upper Albian species that may not bear separation from *O. salasi*.

Collignon (1936) recorded *O. mirapelianum*, *O. colcanapi* Collignon, *O. boulei* Collignon, and *O. bravoense* Collignon (*non* Böse) from the same level and locality (Berambo) in the Middle Albian of Madagascar. His *O. colcanapi* is certainly very close to *O. buarquianum*, although the true affinities of the Madagascan material must await reassessment at the population level.

The species of *Oxytropidoceras* figured by Reyment (1955) from Nigeria are all poorly preserved juveniles with the simple, flexuous ribbing of *O. (Mirapelia)*. Additional and better preserved material is required for a satisfactory identification.

Oxytropidoceras chihuahuaense (Böse) (1910: 73, pl. 5 (figs 3–4), pl. 7 (figs 3–4), pl. 8 (figs 1–2)) was assigned by Young (1966) to *Venezoliceras*, but the absence of a flank tubercle clearly places it in *O. (Mirapelia)*. The lectotype is the original of the specimen figured by Böse (1910, pl. 7 (figs 3–4), pl. 8 (fig. 1)), which shows rather rigid, slightly prorsiradiate single ribs that broaden ventrally and terminate in weak ventrolateral swellings. These features are within the range of variation of the Angolan material, but since Böse's species is, in Texas at least (Young 1966), dated as upper Middle Albian–lower Upper Albian, it is maintained as distinct.

Oxytropidoceras involutum Beurlen is based upon immature material that is very close to typical examples of this species. It is likely to prove a synonym of *O. buarquianum*.

Oxytropidoceras (Mirapelia) sergipense (White, 1887)

Figs 11B, 18A–B, 23E, H, 28

Ammonites sergipensis White, 1887: 221, pl. 24 (figs 1–2).
Pervinquieria sergipensis (White) Maury, 1930: 294; 1936: 236, pl. 24 (figs 3–4).
?Oxytropidoceras buarquianum (White) Maury, 1936: 250, pl. 9 (fig. 1 only).
Oxytropidoceras mauryae Beurlen, 1952: 162, fig. 3.
Dipoloceras sergipense (White) Young, 1966: 20, 22, 24.
Oxytropidoceras (Venezoliceras) sergipense (White) Renz, 1968: 630.
Oxytropidoceras (Androiavites) mauryae Beurlen, 1970: 468, pl. 6 (fig. 1).
Non Mortoniceras sergipensis (White) Beurlen, 1970: 468, pl. 6 (figs 2–4), fig. 19.

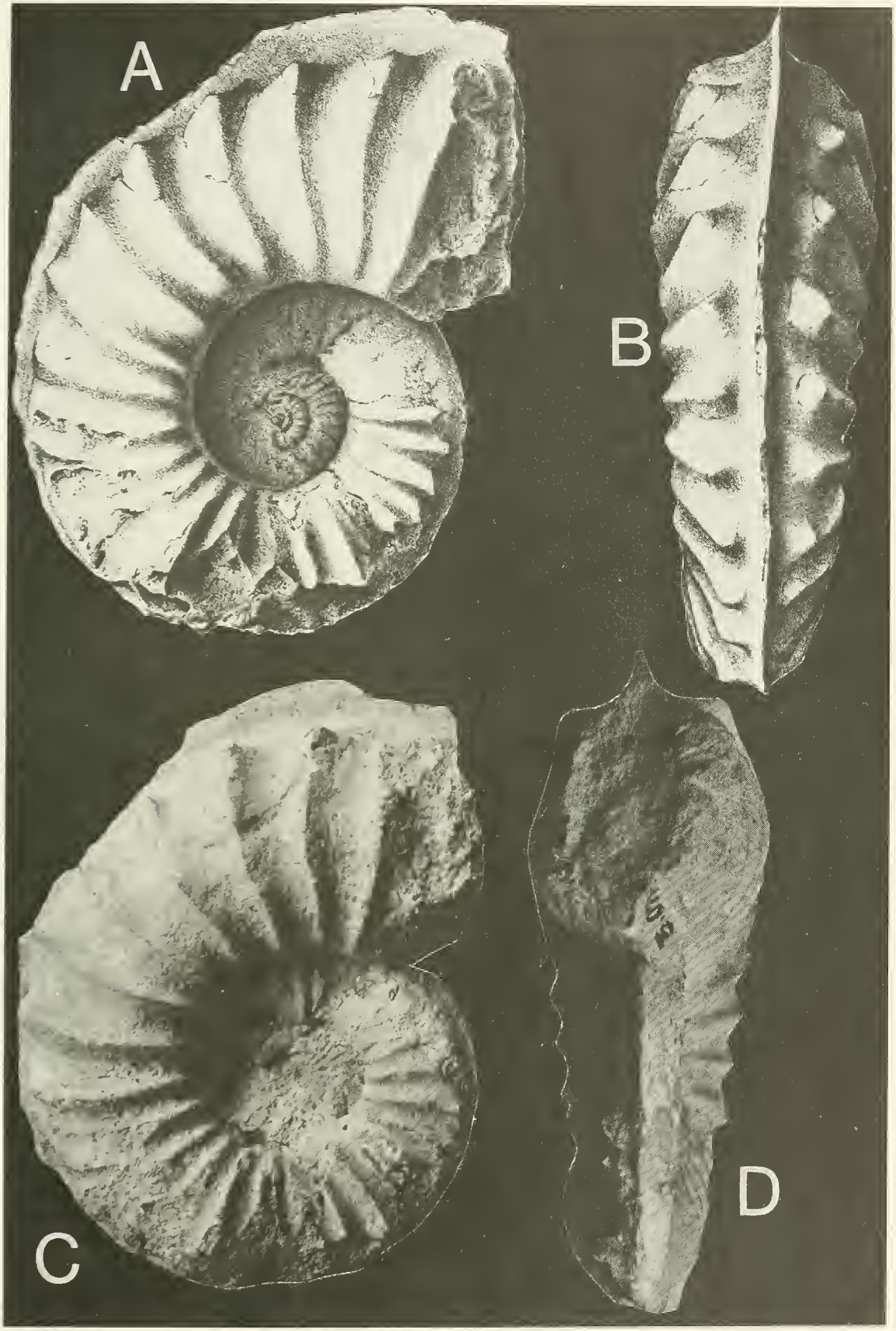

Fig. 28. *Oxytropidoceras (Mirapelia) sergipense* (White). A–B. White's (1887) original illustration. C–D. The original of White's illustration, herein selected as lectotype, in the Natural History Museum, Rio de Janeiro. Photo: P. Bengtson. Both × 1.

Material

Six specimens in the South African Museum, SAM–PCA3755, 3765, and 5444, together with three unnumbered examples. All are preserved as limestone steinkerns.

Description

The shell is rather inflated and moderately evolute, with the outer whorl covering about 25 per cent of the preceding whorl. The umbilicus is moderately wide (32–35% of the diameter) and fairly shallow, with steep umbilical walls and evenly rounded shoulders. Intercostally the whorl section is oval, compressed, whereas costally it is subquadrate (Fig. 23E, H). Ribs begin at the umbilical seam and, across the flank, are slightly flexuous and prorsiradiate, terminating in prominent ventrolateral tubercles that are projected forward on the venter. There are thirty ribs on the outer whorl. The flanks are convex and converge slightly towards the venter, with maximum width about one-third of the way up the flanks. The keel is not preserved but must have stood high above the venter.

Discussion

The confusion surrounding the generic status of White's (1887) species is evident from the synonymy. It is, indeed, very close to *Venezoliceras*, as noted by Renz (1968), but lacks the development of flank tubercles. On the other hand, it is also very similar to the more inflated *Oxytropidoceras douglasi* morphotypes with which it coexists, differing only in the very pronounced development of ventrolateral tubercles. In gross morphology and stratigraphic position, therefore, *O. (M.) sergipense* is intermediate between *O. (Mirapelia)* and *Venezoliceras*. Phylogenetically, it is perhaps worth noting that Young (1966) assigned this species to *Dipoloceras*, while Spath (1932) referred such typical *O. (Mirapelia)* species as *O. evansi* (Spath), and even *O. mirapelianum* (d'Orbigny) itself, to *Dipoloceras*. As such, it seems likely that the origins of *Dipoloceras* also lie in *O. (Mirapelia)* of the *sergipense* group.

Oxytropidoceras (Androiavites) mauryae Beurlen shows the same prominent ventrolateral tubercles and simple ribbing as *O. (M.) sergipense* and is here regarded as conspecific. The specimen figured by Beurlen (1970) is an Upper Albian *Mortoniceras (Angolaites)* with distinct umbilical and doubled ventrolateral tubercles.

Oxytropidoceras (Mirapelia) sergipense (White) is very close to certain species of *Mojsisoviczia* (Figs 20, 22B–C), from which it is readily distinguished by its greater compression and the absence of a lateral tubercle. In this respect the figured but undescribed material of *Mojsisoviczia* aff. *delaruei* (d'Orbigny) (Spath 1930: 61, pl. 9 (figs 13, 16)) closely resembles the present species, since a lateral tubercle is not evident in the illustrations. It seems reasonable to assume that the ancestry of *Mojsisoviczia* lies in *O. (Mirapelia)* of the *sergipense* group.

Fig. 29. *Oxytropidoceras (Oxytropidoceras) boesei* Knechtel, SAM–PCA5452, × 1.

Oxytropidoceras (Oxytropidoceras) boesei Knechtel, 1947

Figs 29–31A

Oxytropidoceras (Manuaniceras) bösei Knechtel, 1947: 109, pl. 27 (fig. 1).
? Manuaniceras uddeni Young, 1966: 95, pl. 12 (figs 1, 4–5), pl. 13 (fig. 1), pl. 16 (figs 1, 3), figs 10b, 12b.

Material

Three specimens, SAM–PCA5452–5453 and an unnumbered example in the South African Museum, preserved as limestone steinkerns.

Description

The Angolan material comprises several rather eroded internal moulds of body chamber fragments that, because of scaphitoid-uncoiling of the body chamber, appear to be more evolute (umbilicus 33% of the diameter) than the earlier growth stages actually were. The shell is strongly compressed, with a lanceolate whorl section (Fig. 30) and broad, convex flanks. Maximum width is about one-third of the way up the flanks. Although the siphonal keel is not preserved, it certainly stood well above the venter.

Ornament comprises dense, flexuous flank ribs that arise at, or close to, the umbilical seam and pass forward across the flanks. The ribs are narrower than the interspaces with a steep, concave, adoral surface and a sloping, convex, adapical face. They frequently bifurcate close to the umbilical seam, but only rarely at, or above, mid-flank. There are 8–9 ribs along the venter in a distance equal to the whorl height. There is no sign of bullae on any part of the flanks.

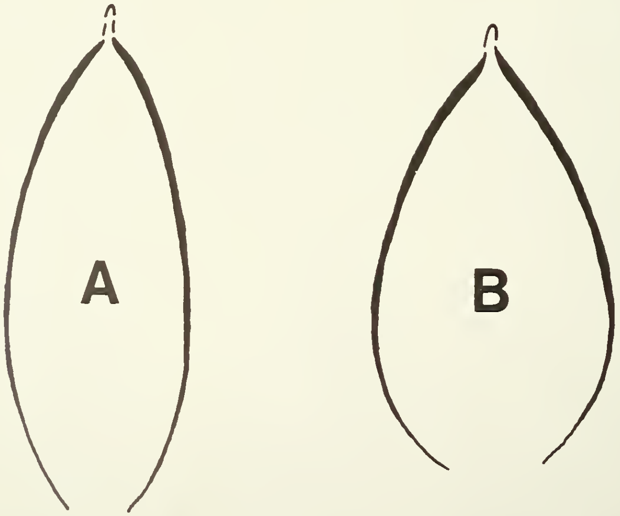

Fig. 30. *Oxytropidoceras (Oxytropidoceras) boesei* Knechtel. Whorl sections. A. SAM–PCA5452. B. SAM–PCA5453. × 1.

Discussion

Oxytropidoceras (Manuaniceras) boesei Knetchel was based upon fragmentary material, without proper description, which shows no features to distinguish it from the Angolan material. The Texas species, *Manuaniceras uddeni* Young, which coexists with *O. (M.) buarquianum*, is very close to the present material. It is said to differ in the presence of a few very weak bullae at the umbilical shoulder, and sometimes also at the point of bifurcation or intercalation of a rib. Since the presence of such bullae is likely to be markedly affected by state of preservation, *M. uddeni* is probably a synonym of *O. boesei*.

Oxytropidoceras roissyanum (d'Orbigny) (Fig. 5A–B) is difficult to compare with the present species because the known material of both species represents vastly different growth stages. So far as can be judged, *O. roissyanum* is much more inflated, with stronger, more robust ribs, about as wide as the interspaces, and does not show bifurcation above the umbilical shoulder. *Oxytropidoceras applanatus* Collignon (1936: 183, pl. 16, (fig. 5)) is doubtfully distinct from *O. roissyanum*.

Oxytropidoceras manuanense (Spath) (1921: 281, pl. 25 (fig. 1)) (Fig. 31B) resembles the present species in lacking flattened ribs, but differs in that nearly all ribs bifurcate at some level on the flanks and in the effacement of ribbing in maturity.

Oxytropidoceras cantianum Spath (Fig. 14F–G) is an Upper Albian (*Dipoloceras cristatum* Zone) species that is based upon a juvenile showing strongly branching ribs. It closely approaches the example figured by Young (1966, pl. 7 (figs 4, 6)) as 'probably *M. carbonarium* (Gabb)', and Owen (1971) seems to be right in regarding it a synonym of *O. carbonarium*.

Oxytropidoceras aroeirium Maury (1936: 251, pl. 26, (fig. 7)) is, to judge from the description, very close to the present species. Unfortunately, the writer has not seen the illustrations of this species and thus further comment is unjustified.

AGE OF THE PRESENT FAUNA

Douvilleiceras mammillatum (Schlotheim) has long been considered diagnostic of the uppermost biostratigraphic zone in the Lower Albian, to which it gives its name. Thus, the rich *Douvilleiceras* faunas from the rest of the world are almost invariably assigned to the zone of *D. mammillatum* and considered to be of late early Albian age. Despite the fact that *Douvilleiceras* has long been known to persist into the Middle Albian (Casey 1962; Owen 1971; Destombes *et al.* 1977), including *D. mammillatum* itself (Fig. 12E–F), this has never been a problem in the boreal realm where the incoming of *Hoplites* forms an easily recognizable and diagnostic base to the Middle Albian. Outside the hoplitinid faunal province, however, no such aid is available and the problem of

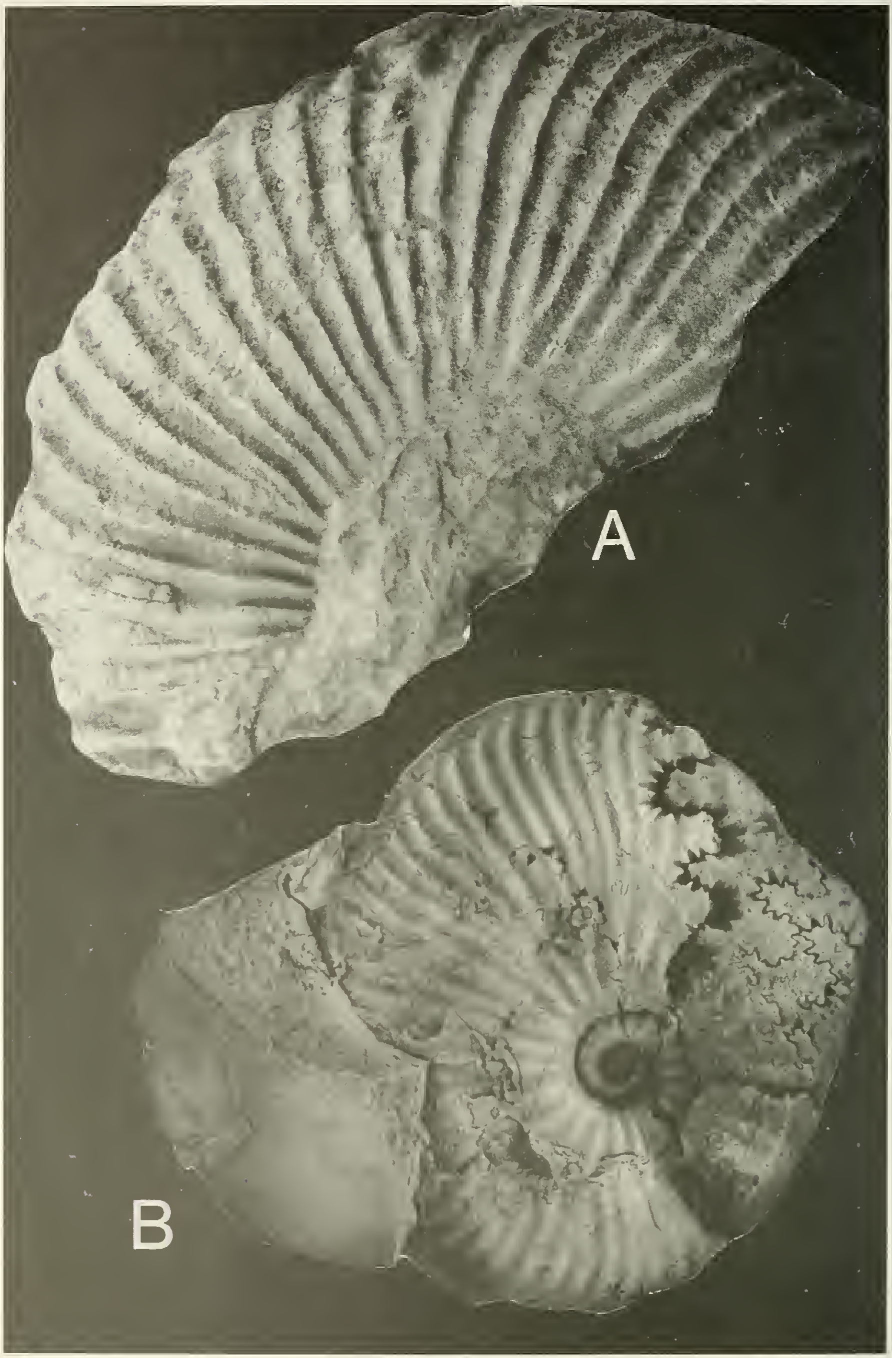

Fig. 31. A. *Oxytropidoceras (Oxytropidoceras) boesei* Knechtel. SAM–PCA5453. B. *Oxytropidoceras (Oxytropidoceras) manuanense* (Spath). SAM–2726, a paratype.

the Lower–Middle Albian boundary is far more complex. These problems led Young (1966) to suggest that *Lyelliceras* may date a younger level in South America than it does in Europe. Contrary to Young's (1966) opinion, however, the writer feels that *Lyelliceras* is critical to the problem of the Lower–Middle Albian boundary, in view of its widespread geographic distribution and common association with hoplitinids in the boreal realm.

In the Anglo-Paris basin, the type region for the Albian Stage, Owen (1971) recognized the following subdivisions of the Middle Albian:

Euhoplites lautus Zone	*Anahoplites daviesi* Subzone
	Euhoplites nitidus Subzone
Euhoplites loricatus Zone	*Euhoplites meandrinus* Subzone
	Mojsisoviczia subdelaruei Subzone
	Dimorphoplites niobe Subzone
	Anahoplites intermedius Subzone
Hoplites dentatus Zone	*Hoplites spathi* Subzone
	Lyelliceras lyelli Subzone
	Isohoplites eodentatus Subzone

In the Anglo-Paris basin, *Douvilleiceras inaequinodum* (Quenstedt) does not range above the *eodentatus* Subzone, while *Oxytropidoceras (Mirapelia) mirapelianum* (d'Orbigny) is a constituent of the *Hoplites spathi* Subzone (Owen 1971). Moreover in Peru, Benavides-Cáceres (1956) records *Oxytropidoceras* '*douglasi*' in association with *Lyelliceras lyelli* (d'Orbigny). There can also be little doubt that the Angolan *Oxytropidoceras* fauna is strictly contemporaneous with those from the Texan zone of *O. salasi*, and it is certainly also represented in Brazil (White 1887; Maury 1936; Beurlen 1970). As such, the *Lyelliceras lyelli* Subzone is represented in the south-central Atlantic region by *Oxytropidoceras buarquianum* (White) and/or *Lyelliceras lyelli* (d'Orbigny), and their associated species. The underlying beds in Angola, dominated by *Douvilleiceras mammillatum aequinodum* (Quenstedt) and *D. inaequinodum* (Quenstedt), are thus certainly to be correlated with the *Isohoplites eodentatus* Subzone of the Anglo-Paris basin. It is perhaps worthy of note that *O. mirapelianum* (d'Orbigny) is a replacement name for *Ammonites cristatus* Quenstedt (*non* DeLuc) and, as such, Quenstedt (1849) was dealing with a faunal horizon closely comparable, and probably strictly contemporaneous, with those at Dombe Grande.

As such, the Dombe Grande faunas are here regarded as of basal Middle Albian age, to be correlated with the *Isohoplites eodentatus* and *Lyelliceras lyelli* Subzones of the European succession. The absence of lyelliceratids and brancoceratids is enigmatic. Since *Oxytropidoceras* species are relatively long-lived, the *Oxytropidoceras (M.) buarquianum* faunule may prove to range somewhat higher. The fact that many of the *Douvilleiceras* assemblages from around the world could now prove to be of basal Middle Albian age suggests that the late early Albian eustatic transgression (Cooper 1977) might actually have peaked during the earliest Middle Albian.

SUMMARY

Two Middle Albian faunules rich in numbers, but poor in species, are described from the vicinity of Dombe Grande, Angola. The lower faunule, which is correlated with the *Isohoplites eodentatus* Subzone of the European sequence has yielded *Douvilleiceras mammillatum aequinodum* (Quenstedt), *D. inaequinodum* (Quenstedt), *D. variabile* Tavani and *Puzosia bistricta* (White). The upper faunule has yielded *Oxytropidoceras (Oxytropidoceras) boesei* Knechtel, *O. (M.) buarquianum* (White), *O. (M.) sergipense* (White), *Puzosia bistricta* (White), *Protanisoceras* sp. and a *Hamites* sp., and is to be correlated with the *Lyelliceras lyelli* Subzone of the Anglo-Paris basin. Mojsisovicziinid phylogeny is discussed, and the following new taxa introduced: *Mortoniceratoides* gen. nov., *Oxytropidoceras (Mirapelia)* subgen. nov. and *O. (Benavidesites)* subgen. nov., while *Manuaniceras* is included in the synonymy of *Oxytropidoceras* s.s.

ACKNOWLEDGEMENTS

I am grateful to Dr W. J. Kennedy for providing me with photographs of D'Orbigny's type material, and to Dr P. Bengtson for photographs of the Brazilian material. I should also like to express my thanks to Dr R. Kirby for allowing me to study his collections from the Middle Albian of France. This paper was much improved by the valuable criticism of Prof. K. Young and Dr P. Destombes.

REFERENCES

Anderson, F. M. 1938. Lower Cretaceous deposits in California and Oregon. *Spec. Pap. geol. Soc. Am.* **16**: 1–339.

Arkell, W. J., Kummel, B. & Wright, C. W. 1957. Mesozoic Ammonoidea. Systematic description. *In:* Moore, R. C., *ed. Treatise on invertebrate paleontology*. Part L. Mollusca 4. Cephalopoda. Ammonoidea: L129–L437. Boulder: Geological Society of America; Lawrence: University of Kansas Press.

Benavides-Cáceres, V. E. 1956. Cretaceous System in northern Peru. *Bull. Am. Mus. nat. Hist.* **108**: 359–493.

Beurlen, K. 1952. A linha de sutura de *Oxytropidoceras*. Contribução ao conhecimento da familia Dipoloceratidae. *Anais Acad. bras. Ciênc.* **24**: 159–169.

Beurlen, G. 1970. A fauna do complexo riachuelo/marium. I. Ammonoidea. *Boln téc. Petrobras, Rio de J.* **11**: 437–482.

Böse, E. 1910. Monografía geológica y paleontológia del Cerro de Muleros circa de cuidad Juárez, estado de Chihuahua y descriptión de la fauna Cretácea de la Encantada, placer de Guadalupe, estado de Chihuahua, Mexico. *Bol. Inst. geol. Méx.* **25**: 1–193.

Breistroffer, M. 1947. Sur les zones d'ammonites dans l'Albien de France et d'Angleterre. *Trav. Lab. géol. Univ. Grenoble* **26**: 1–88.

Casey, R. 1962. A monograph of the Ammonoidea of the Lower Greensand. Part 4. *Palaeont. Soc. Monogr.*: 217–288.

Choffat, P. & Loriol, P. de 1888. Matériaux pour l'étude stratigraphique et paléontologique de la province d'Angola. *Mém. Soc. Phys. Genève* **30**: 1–116.

Collignon, M. 1936. Les *Oxytropidoceras* de l'Albien moyen (niveau supérieur) de la province d'Analalava. *In:* Besairie, H. Recherches géologiques à Madagascar. Première suite. La géologie du nord-ouest. *Mém. Acad. Malgache* **21**: 176–187.

Collignon, M. 1950. Recherches sur les faunes albiennes de Madagascar. 3. L'Albien de Komihevitra. *Annls géol. Serv. Mines Madagascar* **17**: 21–54.

Collignon, M. 1963. *Atlas des fossiles caracteristiques de Madagascar (Ammonites)*. IX. Albien. Tananarive: Service géologique.

Collignon, M. 1966. Les céphalopodes crétacés du bassin côtier de Tarfaya. *Notes Mém. Serv. Mines Carte géol. Maroc* **175**: 1–148.

Cooper, M. R. 1976. The mid-Cretaceous (Albian-Turonian) biostratigraphy of Angola. *Annls Mus. Hist. nat. Nice* **4**: 16.1–16.22.

Cooper, M. R. 1977. Eustacy during the Cretaceous: its implications and importance. *Palaeogeogr., Palaeoclimat., Palaeoecol.* **22**: 1–60.

Destombes, P., Gamble, H. J., Juignet, P. & Owen, H. G. 1977. Cretaceous and Lower Tertiary of Seine-Maritime, France: a guide to key localities. *Proc. Geol. Assoc.* **88**: 15–38.

Douglas, J. A. 1921. Geological sections through the Andes of Peru and Bolivia. III. From the port of Callao to the river Perene. *Q. Jl geol. Soc. Lond.* **77**: 246–284.

Douvillé, R. 1906. Sur les ammonites du crétacé Sud-Américain. *Annls Soc. r. zool. malacol. Belg.* **41**: 142–155.

Howarth, M. K. 1965. Cretaceous ammonites and nautiloids from Angola. *Bull. Br. Mus. nat. Hist.* (Geol.) **10**: 335–412.

Hyatt, A. 1903. Pseudoceratites of the Cretaceous. *Monogr. U.S. geol. Surv.* **44**: 1–351.

Kennedy, W. J. & Cobban, W. A. 1976. Aspects of ammonite biology, biogeography, and biostratigraphy. *Spec. Pap. Palaeont.* **17**: 1–94.

Kennedy, W. J. & Cooper, M. R. 1977. The micromorph Albian ammonite *Falloticeras* Parona and Bonarelli. *Palaeontology* **20**: 793–804.

Knechtel, M. M. 1947. Cephalopoda. Part I. *In:* Knechtel, M. M., Richards, E. F. & Rathbun, M. V. Mesozoic fossils of the Peruvian Andes. *Johns Hopkins Univ. Stud. Geol.* **15**: 81–128.

Maury, C. J. 1930. O Cretáceo da Parahyba do Norte. *Monogr. Serv. geol. min. Brazil* **8**: 1–308.

Maury, C. J. 1936. O Crétaceo de Sergipe. *Monogr. Serv. geol. min. Brazil* **11**: 1–283.

McLearn, F. H. 1972. Ammonoids of the Lower Cretaceous sandstone member of the Haida Formation, Skidegate Inlet, Queen Charlotte Islands, western British Columbia. *Bull. geol. Surv. Canada* **188**: 1–78.

Mirzoyev, G. G. 1967. New species of *Douvilleiceras* from Lower Albian deposits on the southwestern spurs of the Gissar Range. *Paleont. J.* **1**: 53–63.

Neto, M. G. M. 1960. Géologie de la région Benguela-Cuio. *Bolm Serv. geol. min. Angola* **1**: 89–99.

Neto, M. G. M. 1961. As bacias sedimentares de Benguela e Moçâmedes. *Bolm Serv. geol. min. Angola* **3**: 63–93.

Oliveira, A. I. & Leonardos, O. H. 1943. *Geologia de Brasil.* 2nd ed. Rio de Janeiro: Service de Informação Agricola.

Orbigny, A. d'. 1840–41. *Paléontologie française. Terrains crétacés.* I. *Céphalopodes.* Paris: Masson.

Owen, H. G. 1971. Middle Albian stratigraphy in the Anglo-Paris Basin. *Bull. Br. Mus. nat. Hist.* (geol.) Suppl. **8**: 1–164.

Parona, C. F. & Bonarelli, E. G. 1897. Fossili albiani d'Escragnolles, del Nizzardo e della Liguria occidentale. *Palaeontogr. ital.* **2**: 53–112.

Pictet, F. J. & Renevier, E. 1854–9. Description des fossiles du terrain Aptien de la Perte-du-Rhône et des environs de Ste Croix. *Mat. pal. Suisse* **1**: 1–184.

Quenstedt, F. A. 1849. *Petrofacten Deutschlands.* I. *Cephalopoden.* **6**: 473–580. Tubingen.

Renz, O. 1968. Über die Untergattungen *Venezoliceras* Spath und *Laraiceras* n.subgen. der Gattung *Oxytropidoceras* Stieler (Ammonoidea) aus den Venezolanischen Anden. *Eclogae geol. Helv.* **61**: 615–655.

Reyment, R. A. 1955. The Cretaceous Ammonoidea of southern Nigeria and the southern Cameroons. *Bull. geol. Surv. Nigeria* **25**: 1–112.

Scott, G. 1937. Ammonites of the genera *Sonneratia* and *Douvilleiceras* from the Cretaceous of Colombia. *J. Paleont.* **11**: 34–37.

Scott, G. 1940. Cephalopods from the Cretaceous Trinity Group of the south-central United States. *Univ. Texas Publ.* **3945**: 969–1106.

Spath, L. F. 1921. On the Cretaceous Cephalopoda from Zululand. *Ann. S. Afr. Mus.* **12**: 217–321.

Spath, L. F. 1923–43. A monograph of the Ammonoidea of the Gault. *Palaeont. Soc. Monogr.*: 1–787.

Spath, L. F. 1930. The fauna of the Samana Range and some of the neighbouring areas. The Lower Cretaceous Ammonoidea, with notes on the Albian Cephalopoda from Hazara. *Mem. geol. Surv. India palaeont. indica* (n.s.) **15**: 51–66.

Tavani, G. 1942. Paleontologia della Somalia. III. Fossili del Cretaceo. 6. Molluschi del Cretaceo della Somalia. *Palaeontogr. ital.* **32** (4): 7–47.

Tavani, G. 1949. Fauna malacologica Cretacea della Somalia e dell'Ogaden. 2. Gastropoda—Cephalopoda—conclusioni. *Palaeontogr. ital.* **45**: 1–76.

White, C. A. 1887. Contribuções a palaeontologia do Brazil. *Archos Mus. nac., Rio de J.* **7**: 1–273.

Young, K. 1966. Texas Mojsisovicziinae (Ammonoidea) and the zonation of the Fredricksburg. *Mem. geol. Soc. Am.* **100**: 1–225.

Young, K. 1974. Lower Albian and Aptian (Cretaceous) ammonites of Texas. *Geosci. Man* **8**: 175–228.